

One of the greatest icons of evolution in archaeology field is called Australopithecus afarensis or “Lucy”. It is a collection of several hundred pieces of fossilized bone representing 40 percent of a female of the hominin species Australopithecus afarensis. In Ethiopia, the assembly is also known as Dinkinesh. But is she really a human ancestor? After recent studies published by many famous magazines like PNAS, it became obvious that Lucy is just a bedtime story. The study says that this specie is just another extinct specie of gorillas. They found that the Mandibular ramus morphology on a recently discovered specimen of Australopithecus afarensis closely matches that of gorillas, and is different from the one of humans and the supposed relatives, chimpanzees.

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Gorilla-like anatomy on *Australopithecus afarensis* mandibles suggests *Au. afarensis* link to robust australopiths

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Abstract

Mandibular ramus morphology on a recently discovered specimen of *Australopithecus afarensis* closely matches that of gorillas. This finding was unexpected given that chimpanzees are the closest living relatives of humans. Because modern humans, chimpanzees, orangutans, and many other primates share a ramal morphology that differs from that of gorillas, the gorilla anatomy must represent a unique condition, and its appearance in fossil hominins must represent an independently derived morphology. This particular morphology appears also in *Australopithecus robustus*. The presence of the morphology in both the latter and *Au. afarensis* and its absence in modern humans cast doubt on the role of *Au. afarensis* as a modern human ancestor. The ramal anatomy of the earlier *Ardipithecus ramidus* is virtually that of a chimpanzee, corroborating the proposed phylogenetic scenario.

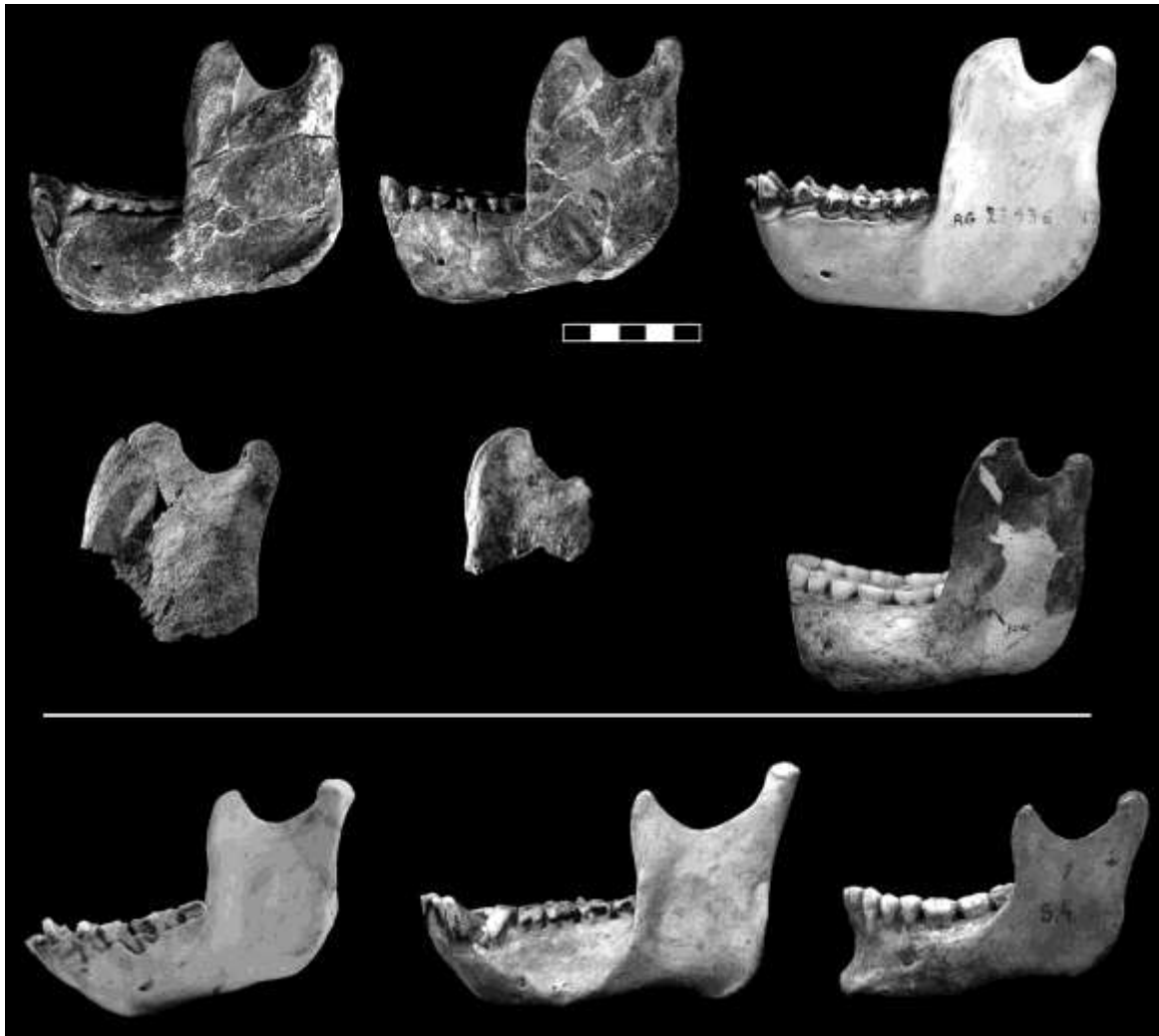
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In all primates, the superior end of the mandibular ramus terminates in two processes: posteriorly, the condylar process, which articulates with the base of the skull, and anteriorly, the coronoid process, which is the insertion site of the temporalis muscle. An indentation, the mandibular (or sigmoid) notch, separates these two processes.

Among extant higher primates, each species shows species-specific characteristics of the ramus. Nevertheless, the ramal configurations in those primates that we studied clearly fall into two groups: one consists of gorillas, and the other consists of modern humans, two chimpanzee species, and orangutans. In the latter group, which shares a pattern of ramal morphology with many other primates that we examined, the coronoid process is typically lower than the condylar process; the base of the coronoid constitutes a relatively small percentage of the ramal width and tapers into a slender, pointed, superiorly directed tip ([Fig. 1](#)). This tapering produces a spacious mandibular notch between the two processes; hence, the deepest point of the notch is situated anteriorly. In gorillas, on the other hand, the coronoid process is usually higher than the condylar process. The broad base of the coronoid constitutes much of the ramal width, moving the deepest point of the mandibular notch closer to the condylar process than in what we interpret to be the more primitive (common) configuration. With the tip of the coronoid pointing posteriorly, the superior edge of the process in gorillas assumes a flat contour; in many cases, the tip overhangs the mandibular notch, lending the process a hook-like appearance, and the notch, a narrow, deep, confined appearance. As a consequence, the notch occupies a smaller portion of the total ramal area than in the more common ramal morphology.[§]

Fig. 1.



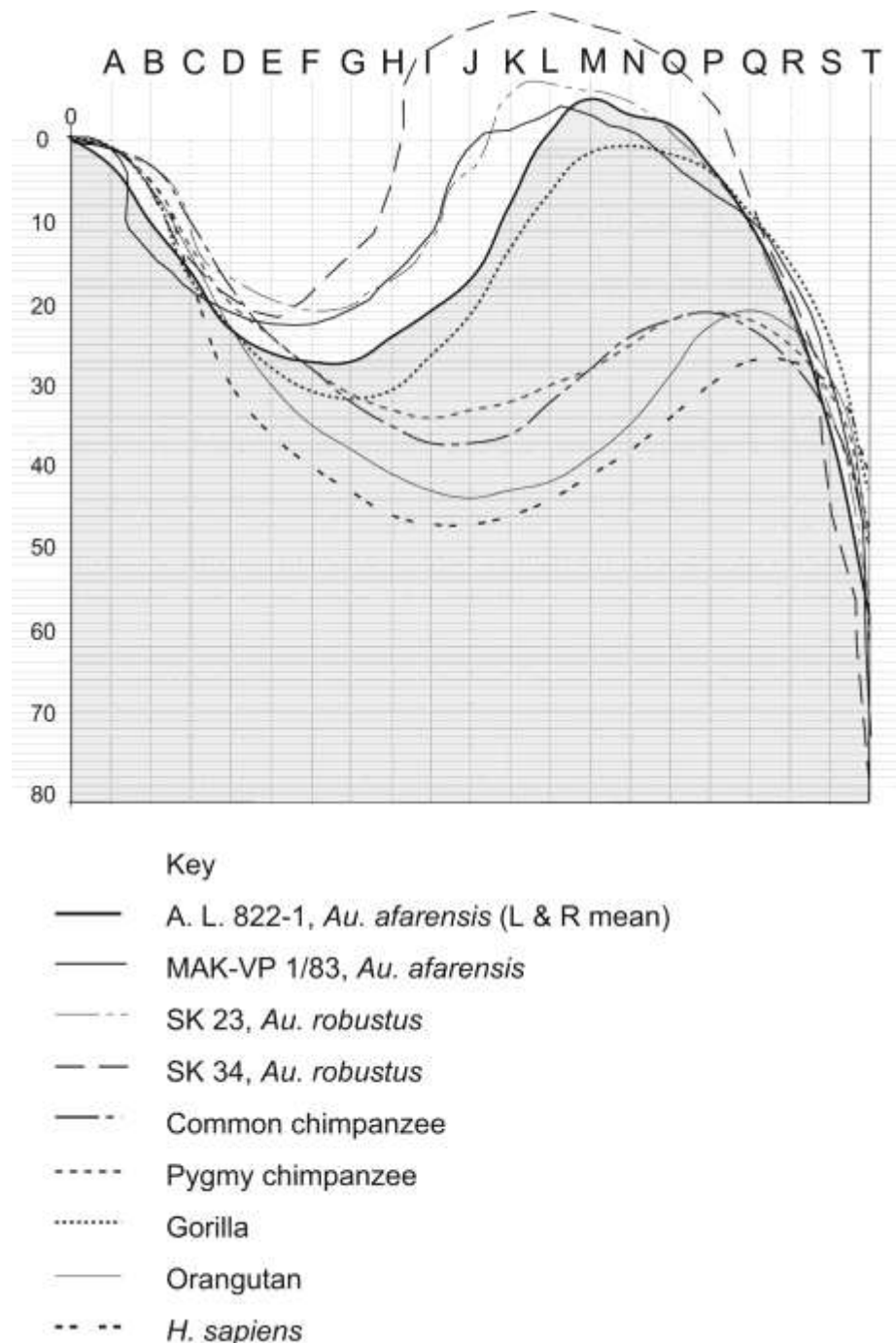
Ramal morphology in *Au. afarensis* and extant primates. (Top) Left mandibular ramus and right mandibular ramus (horizontally flipped) of *Au. afarensis* specimen A. L. 822-1 and left mandibular ramus of a gorilla. (Middle) Left mandibular ramus of *Au. afarensis* MAK-VP 1/83 specimen; fragment of left mandibular ramus of *Au. afarensis* specimen A. L. 333-100; and mandibular ramus of *Au. robustus* specimen SK 23. (Bottom) Mandibular ramus of a chimpanzee, an orangutan, and *H. sapiens*. (Scale bar: 5 cm.) Note that the upper end of the ramus in all of the specimens above the white line resembles that of a gorilla (particularly in the shape of the coronoid, the great percentage that the coronoid base constitutes of the ramal width, the confined appearance of the mandibular notch, and the small percentage that the notch area constitutes of the ramal area). The limited reconstruction of the coronoid process on the left ramus of A. L. 822-1 is based on the corresponding preserved area on the right ramus and vice versa.

The ramus of an *Australopithecus afarensis* specimen discovered in 2002, A. L. 822-1 ([Fig. 1](#)), closely matches that of the gorilla. The specimen is a fragmentary but well preserved skull of an adult individual found in the Unda Hadar, a tributary of the Awash River running parallel to the Kada Hadar. Discovered ≈ 2.5 km east of A. L. 288 (Lucy's site), the specimen was recovered from the lower Kada Hadar member and is ≈ 3.1 million years old. Its calvarial, facial, mandibular, and dental morphologies demonstrate that the specimen belongs to *Au. afarensis*.[¶]

To quantify the contour of the essentially two-dimensional structure that lies between the posterior ramal margin and the parallel, anterior ramal margin, we plotted each ramus in our fossil and extant primate samples on a fixed, specifically constructed system of coordinates.

In this procedure, the contour of each ramus is expressed as 20 numeric values referenced to the coordinate system [[supporting information \(SI\) Table 1](#); see *Materials and Methods* for details] from which a mean contour could be calculated for each taxon ([Fig. 2](#)). This procedure enabled us to perform statistical analyses of ramus shape.

Fig. 2.



The mean contour of the superior margins of the left and right mandibular ramus in A. L. 822-1 compared with the mean contours of other primates. The A. L. 822-1 contour constitutes the border of the shaded area. Note that the contours fall into two distinct groups. Each contour was plotted with the posterior margin of the ramus vertically oriented. The tip of each condylar process lies at the upper left corner of the coordinate system (the zero point), and the anterior margin of the ramus lies at the far right, at the vertical line T. These contours do not express the posteriorly directed tip of the coronoid process (see [Fig. 1](#))

exhibited by A. L. 822-1 and many gorillas; the resolution of the grid does not capture the full extent of the tip's morphology.

We performed a discriminant function analysis (1, 2) on the 20 ramal shape variables. The Kolmogorov–Smirnov normality test showed that all of the variables, except for the first two, were distributed normally. On the basis of posterior probabilities, we classified all of the mandibles to taxon and identified misassigned cases. A classification matrix summarizes these results (SI Tables 2 and 3).

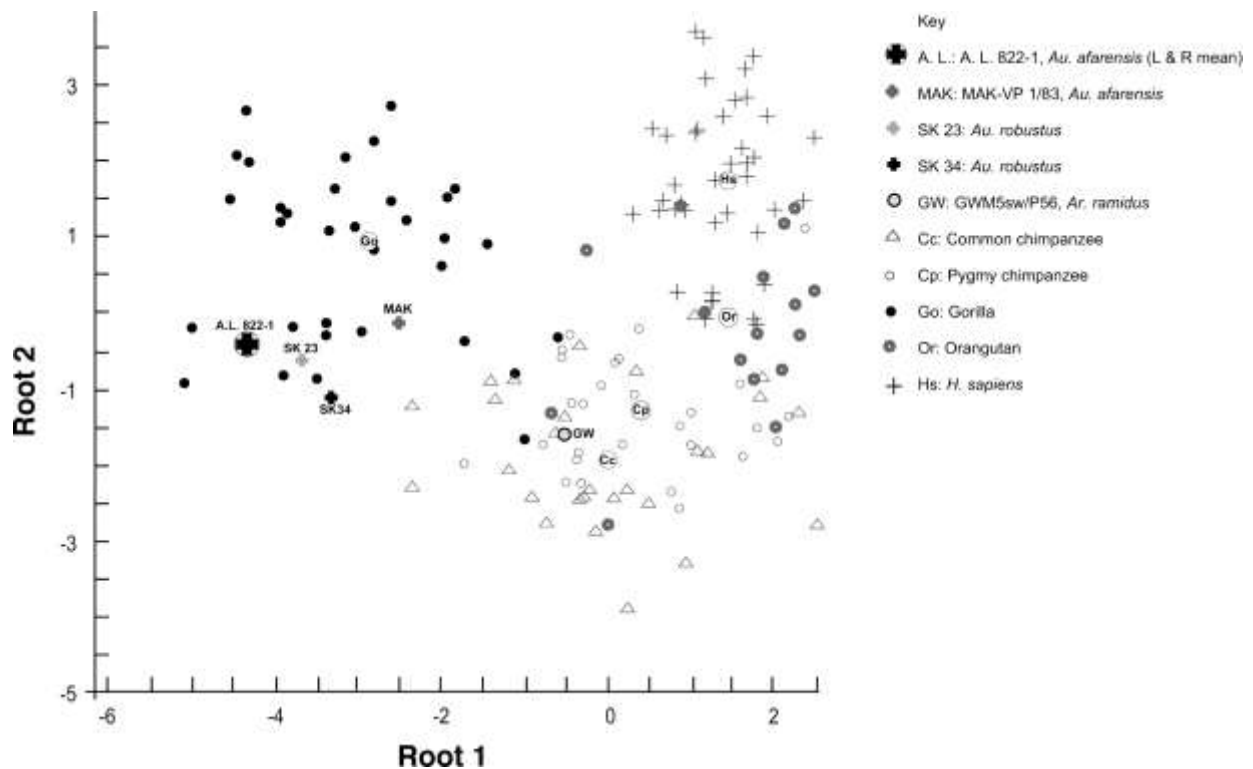
Results

The analysis of variance reveals that group centroids of the extant great ape species differ significantly [Wilk's $\lambda = 0.048$, $F_{(80, 483)} = 7.04$, $P < 0.0001$]. Post hoc tests among group means show a significant difference between all pairwise combinations [$F_{(20, 122)} \geq 1.89$, $P < 0.02$ in all comparisons]. The least different were the two species of chimpanzees, *Pan troglodytes* and *Pan paniscus* [$F_{(20, 122)} = 1.89$, $P < 0.02$]. [The other 14 pairwise comparisons yielded $F_{(20, 122)}$ ranging from 3.18 to 15.52; $P < 0.005$ in all comparisons.] The greatest differences were observed between gorillas and all of the other species.

The *a priori* classification probability was determined on the basis of group size (that is, the calculation took into account the differences between the sample sizes of the species). The final classification matrix shows an overall classification success of 82%. Modern humans were correctly assigned in 93% of the cases. Not unexpectedly, the highest percentage of assignment errors (31%) occurred with common chimpanzees, with a classification success of only 69%; most of the misassigned individuals were assigned as pygmy chimpanzees.

The first two canonical variables account for 89% of the variance (50% and 39%, respectively). The variables *N* and *G* constitute the highest loads in the first and second factor, respectively. These two variables roughly correspond to the high point of the coronoid process and the low point in the mandibular notch in the ramal contour (see Fig. 2). Fig. 3 presents a scatterplot of the first two canonical roots. *Au. afarensis* was initially considered an unknown in the analysis, so its position in the plot and its probability of assignment were calculated subsequently, according to the predetermined classification functions. The posterior probability for *Au. afarensis* is highest with gorillas, at 99.9% for A. L. 822-1 and 92.7% for another *Au. afarensis* mandible, MAK-VP 1/83 (Fig. 1), a specimen from the Maka sands in the Middle Awash, Ethiopia (3). Although less complete, this specimen retains sufficient morphology for quantification. The visual resemblance between the ramal anatomy of *Au. afarensis* and that of gorillas is confirmed by the morphometric analysis, as are the anatomical differences between this species pair and the other extant species in our sample. Only a small overlap exists between the gorilla cluster and the chimpanzee cluster (Fig. 3 shows the canonical scores of individual specimens); nevertheless, the two *Au. afarensis* specimens fall within the gorilla area, clearly outside the area of overlap.

Fig. 3.



Canonical scores of root 1 versus root 2. Individual scores are indicated by species-specific symbols, and group centroids are indicated by encircled species-specific abbreviations. Roots 1 and 2 account for 50.2% and 38.8% of the variance, respectively.

Although only A. L. 822-1 and MAK-VP 1/83 are complete enough to be analyzed by the method used here, the same ramal anatomy is evident on other *Au. afarensis* specimens that are more fragmentary: A. L. 333-100, from the Hadar site in Ethiopia (4) (Fig. 1); A. L. 333w-15, a small fragment that is probably pathological; and the meager remains of the mandibular notch in A. L. 438-1g, A. L. 333-108, and A. L. 288-1i (Lucy). Until the discovery of A. L. 822-1, the resemblance of these specimens to gorillas went unnoticed even though the specimens have been known of for many years.

Even very young *Au. afarensis* individuals, such as A. L. 333-43b (SI Fig. 4) and the newly discovered, less complete A. L. 333n-1, exhibit a similar morphology to that of gorillas of comparable age and differ from young individuals of the other primate species that we studied. Thus, no significant ontogenetic change is evident in the shape of the superior portion of the mandibular ramus.

The observed interspecific differences in ramal morphology are not due to the relative size and orientation of the temporalis muscle, which can be deduced from differences in the osteological calvarial landmarks related to the origin of the temporalis: the height and length of the sagittal crest, the extent and size of the temporal/nuchal (T/N) compound crest, and the size of the “bare area” between the temporal and nuchal lines (5). Male and female gorillas, for example, differ considerably in these indicative exocranial landmarks but display the same ramal morphology. Female gorillas and male and female chimpanzees have a similar cranial creasing pattern, yet they differ substantially in ramal morphology. Although *Au. afarensis* resembles chimpanzees (and female gorillas) in its creasing pattern (5), the *Au. afarensis* mandibular ramal morphology resembles that of gorillas, not chimpanzees.

The similarity between gorillas and *Au. afarensis* in ramal morphology does not appear to be the outcome of similar selective pressures, because these two species differ in habitat (6–9) and diet. [Evidence of the latter derives from studies of differences in tooth enamel thickness,

the topography of the occlusal surfaces, and the shape of the dental arcade in gorillas and in *Au. afarensis* (3, 4, 9–13).]

We note again that orangutans, the outgroup in the analysis, fall within the generalized group. The contour of the superior portion of the ramus in orangutans is much more similar to that of modern humans and chimpanzees than to the gorilla contour (Figs. 1–3).

Significantly, the ramal anatomy observed in *Au. afarensis* and gorillas is present also in the only two *Au. robustus* specimens that are complete enough to permit examination of the ramus: SK 23 (Figs. 1–3) and SK 34 (Figs. 2 and 3 and SI Fig. 4). The posterior probability of SK 23 is highest with gorillas, at 97.4%, as is that of SK 34, at 55.2% (SI Table 3). Even more importantly, when we assign the *Au. robustus* specimens as the sixth (known) classification group, the posterior probabilities for A. L. 822-1 (99.9%) and the Maka mandible (97.9%) are highest for *Au. robustus*. In other words, the superior ramal contours of *Au. afarensis* and *Au. robustus* are virtually identical. Before the analysis of *Au. afarensis* reported here, this ramal morphology went practically unnoticed in *Au. robustus* (but see Robinson, ref. 14, page 226).

Discussion and Conclusions

Given a phylogeny in which chimpanzees and modern humans are sister groups, parsimony dictates that we view the similarity in ramal morphology between *Au. afarensis* and gorillas as a homoplastic character, a character that appears independently and as such has no phylogenetic value.

The ramal morphology of modern humans and chimpanzees clearly represents the primitive condition, because this morphology closely matches that of orangutans, the outgroup in this analysis, and is shared by many other primates, as can be observed visually.

Thus, the *Au. afarensis* ramal morphology is a novelty that appeared independently in gorillas and hominins. In the latter, this morphology constituted at first an autapomorphic (unique) trait and eventually became a synapomorphic (shared derived) trait that unites *Au. afarensis* and *Au. robustus* into a single clade (which possibly includes all of the robust australopiths, although no *Australopithecus boisei* or *Au. aethiopicus* specimens exhibiting this region are available at present). Nonetheless, the morphology of the *Au. afarensis* face (5, 15) and dentition (4) still represents the most generalized state in the robust morphocline of these characters. For those who advocate the inclusion of *Au. africanus* in the robust clade (15–17), it is significant that Sts 7, the only *Au. africanus* specimen that permits the relevant observation, although still embedded in breccia, exhibits the same ramal morphology as *Au. robustus* and *Au. afarensis* (see figure 21 on Plate 5 in ref. 18).

The *Au. afarensis* ramal morphology can be added to other traits that this species shares with *Au. robustus* (5) and casts doubt on the postulated role of *Au. afarensis* as the common ancestor of later hominins (15, 17, 19). *Au. afarensis* is simply too derived to occupy a position as a common ancestor of both the *Homo* and robust australopith clades. Claims that *Au. afarensis* is too derived to fulfill this role have, indeed, been voiced sporadically ever since this species was recognized (20–23).

If one accepts the gorilla–*Au. afarensis* ramal morphology as homoplasy, one may legitimately ask why we consider the resemblance between *Au. afarensis* and *Au. robustus* a synapomorphy rather than homoplasy. The answer is that, in the gorilla–hominin case, we are equipped with all of the genetic evidence supporting the claim of homoplasy, whereas such evidence is unavailable in the fossil hominins that exhibit the gorilla-like ramal morphology. Hence, claiming synapomorphy within the latter group is a simpler solution. Furthermore, synapomorphy aside, even if the presence of similar ramal morphology in *Au. afarensis* and

Au. robustus did, indeed, represent homoplasy, the *Au. afarensis* ramal anatomy would still exclude this taxon from our ancestry.¹

Additional support for the phylogenetic hypothesis proposed here comes from another early hominin, *Ardipithecus ramidus*, whose ramus was recently unearthed at an Ethiopian site dated at 4.51–4.32 million years ago (ref. 24 and figure 3 therein). In our analysis, the specimen's posterior probability is highest with chimpanzees, at 98% (Fig. 3 and SI Tables 2 and 3). In other words, the *Ar. ramidus* ramal morphology is almost identical to that of a chimpanzee and thus constitutes further evidence that this morphology is primitive for the chimpanzee and human clade.**

Materials and Methods

We examined a total of 146 extant primate specimens: 41 modern *Homo sapiens* specimens, 31 gorillas (*Gorilla gorilla*), 29 pygmy chimpanzees (*P. paniscus*), 29 common chimpanzees (*P. troglodytes*), and 16 orangutans (*Pongo pygmaeus*). All of the specimens were mature individuals. The modern human specimens come from varied regions: Australia, India, the Levant, and northern Canada (Eskimos).

To convey the anatomical differences in the upper ramal contour, we adopted a method based on Rak *et al.* (27), which consisted of capturing a digital image of the mandibular ramus with the camera centered at the vertical level of the mandibular notch and held perpendicular to the lateral surface of the ramus. Using FreeHand 9.0 for Macintosh (Adobe Systems, Seattle, WA), we traced the digital image of each ramus from the tip of the condylar process to the anterior margin of the ramus. (This step represents a slight modification of the original method, in which the contour extended only as far as the coronoid tip.)

With the aid of the FreeHand software, we stretched the contour proportionally on the vertical and horizontal axes by dragging the contour's lower right corner until it occupied the entire width of the area of the fixed coordinates in the background template. This part of the procedure eliminated differences in size in the analysis. The posterior margin was aligned with the vertical line at 0, and the anterior margin was aligned at T. The posterior ramal margin in the entire sample exhibits a slight concavity between the posterior end of the condyle and the insertion site of the posterior fibers of the masseter and medial pterygoid muscles; using these two posteriorly protruding structures, we were able to orient the posterior margin on a vertical line throughout the sample. The intersection of the ramal contour with each of the vertical lines, A through T, yielded 20 numeric variables for each ramus (SI Table 1).

The decision to position the mandible with the posterior margin of its ramus oriented vertically was based on our observation that this orientation varies the least in reference to the Frankfurt horizontal (the ground) within and between species (SI Fig. 5). In addition, this choice permits us to include two important fragmentary fossils that lack all landmarks except the posterior margin of the ramus: the *Au. afarensis* MAK-VP 1/83 mandible and the *Ar. ramidus* mandible.

One author, A.G., carried out the entire measurement procedure. To evaluate the accuracy of the method, we repeated the procedure on 20 randomly selected mandibles from the modern *H. sapiens* sample and compared the two sets of readings. The second set differed insignificantly from the first, with a discrepancy of 1.7% between the sums of the values of the two full data sets.

We performed the discriminant and variance analyses with STATISTICA for Macintosh (version 4.0; StatSoft, Tulsa, OK).

The second fossil we have is “Homo habilis”. Many people would think that this fossil is a complete fossil with all the details needed to classify it as human ancestor, but that’s only on social media. In reality, it is just a part of a foot and upper half of a skull. To this moment, scientists are still debating the origin of this fossil, unlike we see in propaganda. These disagreements are open to the public in the most notable scientific magazine in the world “Nature”, but people prefer science-fiction over looking up the real science. Let’s see what scientists think about this fossil...

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Human evolution: Fifty years after *Homo habilis*

- [Bernard Wood](#)

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Bernard Wood explains why the announcement of 'handy man' in April 1964 threw the field of hominin evolution into a turmoil that continues to this day.



The foot of 'handy man', *Homo habilis*. Credit: Natural History Museum/Mary Evans Picture Library

Half a century ago, the British–Kenyan palaeoanthropologist Louis Leakey and his colleagues made a controversial proposal: a collection of fossils from the Great Rift Valley in Tanzania belonged to a new species within our own genus¹. The announcement of *Homo habilis* was a turning point in palaeoanthropology. It shifted the search for the first humans from Asia to Africa and began a controversy that endures to this day. Even with all the fossil evidence and analytical techniques from the past 50 years, a convincing hypothesis for the origin of *Homo* remains elusive.

In 1960, the twig of the tree of life that contains hominins — modern humans, their ancestors, and other forms more closely related to humans than to chimpanzees and bonobos — looked remarkably straightforward. At its base was *Australopithecus*, the apeman that palaeoanthropologists had been recovering in southern Africa since the 1920s. This, the thinking went, was replaced by the taller, larger-brained *Homo erectus* from Asia, which spread to Europe and evolved into Neanderthals, which evolved into *Homo sapiens*. But what lay between the australopiths and *H. erectus*, the first known human?

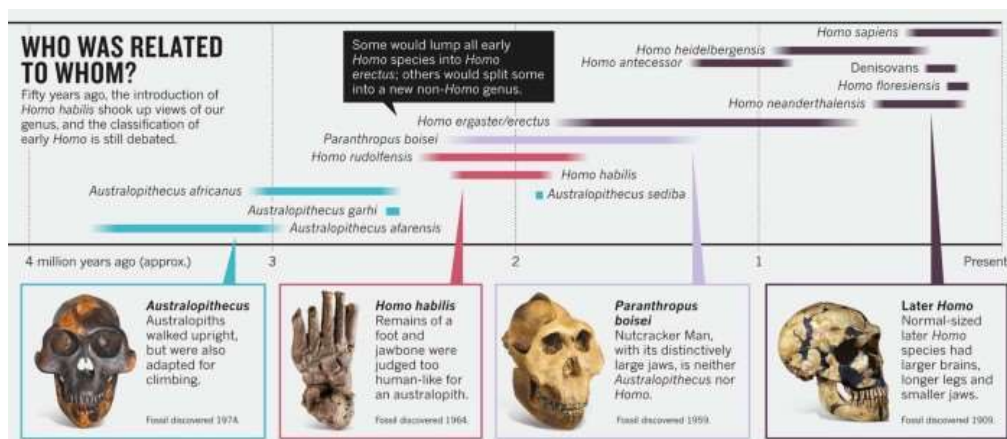
Betting on Africa

Until the 1960s, *H. erectus* had been found only in Asia. But when primitive stone-chopping tools were uncovered at Olduvai Gorge in Tanzania, Leakey became convinced that this is where he would find the earliest stone-tool makers, who he assumed would belong to our genus. Maybe, like the australopiths, our human ancestors also originated in Africa.

In 1931, Leakey began intensive prospecting and excavation at Olduvai Gorge, 33 years before he announced the new human species. Now tourists travel to Olduvai on paved roads in air-conditioned buses; in the 1930s in the rainy season, the journey from Nairobi could take weeks. The ravines at Olduvai offered unparalleled access to ancient strata, but fieldwork was no picnic in the park. Water was often scarce. Leakey and his team had to learn to share Olduvai with all of the wild animals that lived there, lions included.

They found the first trace of the potential toolmaker, two hominin teeth, in 1955. But these were milk teeth, which are not as easy to link to taxa as permanent teeth. The team's persistence was rewarded in 1959, when archaeologist Mary Leakey, Louis's wife, recovered the cranium of a young adult. The specimen still boggles the mind because it is so strange: its small brain, large face, tiny canines and massive, thumbnail-sized chewing teeth were not at all like those of *H. erectus*. Its big molars earned it the nickname 'Nutcracker Man'.

Because Nutcracker Man was found in the same layers as the stone tools, the Leakeys assumed that it was the toolmaker, despite its odd appearance. But when Louis announced the discovery, he was not tempted to expand the definition of *Homo*. That would have eliminated any meaningful distinction between humans and australopiths. Instead he erected a new genus and species, *Zinjanthropus boisei* (now called *Paranthropus boisei*), to accommodate it (see 'Who was related to whom?').



Credit: Australopithecus: Sabena Jane Blackbird/Alamy; H. habilis: Human Origins Program/Smithsonian Institution; P. boisei: Natural History Museum/SPL; H. neanderthalensis: Javier Trueba/MSF/SPL

In 1960, Jonathan Leakey, Louis and Mary's eldest son, found the lower jaw and the top of the head of a juvenile hominin. Dubbed Johnny's Child, it very definitely did not belong to the same species as 'Zinj', and the Leakeys began to suspect that it was the real toolmaker.

Phillip Tobias, a palaeoanthropologist known for his work in South Africa, had already been recruited to analyse Zinj, so the Leakeys turned to him to analyse the juvenile cranium. John Napier, a specialist in hand anatomy (as well as sleight-of-hand magic tricks) was recruited to examine wrist and hand bones found with the skull.

An adult foot was excavated along with Johnny's Child, and three years later, a cranium with both the upper and lower jaw was uncovered, as was a very fragmented cranium with well-preserved teeth. Napier had already convinced himself that the juvenile hand bones were like those of modern humans. My PhD supervisor, Michael Day at the University of London had come to the same conclusion about the foot. And Tobias was certain that neither the long crowns of the chewing teeth in the lower jaw nor the large brain case could belong to the australopiths known from southern Africa.

Handy hypotheses

Thus, in a paper published in *Nature* in April 1964 (ref. [1](#)), Louis, Tobias and Napier made the case for adding the 'handy man' to the genus *Homo* as *H. habilis*. They argued that the Olduvai fossils met three key criteria set out in an influential 1955 definition of *Homo*²: an upright posture, a bipedal gait and the dexterity to fashion primitive stone tools. The team had to relax a brain-size criterion to accommodate the smaller brain (around 600 cubic centimetres) of *H. habilis*.

The proposal was met with considerable scepticism. Some thought that the fossils were too similar to *Australopithecus africanus* to justify a new species. John Robinson, a leading authority on australopiths, suggested that *H. habilis* was a mix of earlier *A. africanus* and later *H. erectus* bones. Other researchers agreed that the species was new. Very few accepted that it was the earliest human.

Subsequent finds shaped the debate. A crushed cranium (dubbed Twiggy) from the lowest strata at Olduvai nixed Robinson's argument that *H. habilis* was a mix of an australopith and *H. erectus*. Another skeleton indicated that *H. habilis* had a stronger and relatively longer (or more ape-like) upper limb than did *H. erectus* and its ilk.

A handful of additional specimens from Ethiopia to South Africa have since been added to *H. habilis*; the biggest contribution to early *Homo* has come from Koobi Fora in Kenya. I have been involved with *H. habilis* for all but two of its 50 years, starting in 1966, when I analysed the ankle bone excavated alongside Johnny's Child. Far from being like that of modern humans, the bone is a much better match for an australopith. Other features of *H. habilis* have also turned out to be less like those of modern humans than Louis and his team suggested.

In the mid-1970s, Louis and Mary's second son, Richard, offered me the challenge of making sense of the early *Homo* skulls, crania and jaws from Koobi Fora. It was a lonely task

involving 15 years poring over australopiths and *H. erectus* fossils in museums around the world. It was tempting to focus on the better-preserved specimens, but more often than not it was a skull fragment here or a broken tooth there that provided the key clues to making sense of the whole collection.

Variation in the Koobi Fora fossils was not so easily shoe-horned into a single species as those from Olduvai³. I concluded that there were two distinct types of face within early *Homo*⁴, and so in 1992, I suggested that a second early *Homo* species, *Homo rudolfensis*, should be recognized⁵. Two decades later, a team led by palaeontologist Meave Leakey (Richard's wife) confirmed⁶ the 'two-taxon' hypothesis I had proposed, using a face and two lower jaws found at Koobi Fora. But they — correctly, I believe — refuted my suggestion about which jaws went with which faces. As ever in palaeontology, new fossils test and refine old ideas.

Drawing the line

In 1999, British anthropologist Mark Collard and I looked⁷ afresh at the boundary between *Homo* and more-primitive hominins by focusing on features that hint at body size, posture, locomotion, diet and life history. For example, how long is the upper limb compared with the lower, or the forearm compared with the upper arm? Do molar teeth erupt early, as in apes, or form slowly and dawdle in the jaw, as in modern humans? All are attributes that help to reveal how an animal makes its living and allocates its energy.

Although *H. habilis* is generally larger than *A. africanus*, its teeth and jaws have the same proportions. What little evidence there is about its body shape, hands and feet suggest that *H. habilis* would be a much better climber than undisputed human ancestors. So, if *H. habilis* is added to *Homo*, the genus has an incoherent mishmash of features. Others disagree, but I think you have to cherry-pick the data⁸ to come to any other conclusion. My sense is that handy man should belong to its own genus, neither australopith nor human.

Beautifully preserved fossils from the Caucasus have now been added to the mix. Just last year, Georgian anthropologist David Lordkipanidze and his colleagues reported⁹ their analysis of five hominin crania recovered from Dmanisi, a spectacular site on a promontory between two rivers in southern Georgia. They concluded that the range of shapes among these skulls equals or exceeds the variation across *H. habilis*, *H. rudolfensis* and *H. erectus*, and on that basis proposed that all *H. habilis*-like fossils be reassigned to *H. erectus*, subsuming three species into one.

Even if you accept that their methods of data capture are sound — which I do not — I question their conclusions. Their method fails to distinguish between a distinctive and large-brained Neanderthal cranium and one of the small-brained Dmanisi skulls, specimens that are separated by close to two million years of evolutionary history. They also take the overall shape of the head to be the arbiter of early hominin taxonomy, yet what sets *H. habilis* and *H. erectus* apart are many finer details, such as the size and shape of the inner ear, features of the hands and feet, the strength of long bones and life history. It is equally plausible that the Dmanisi fossils sample a hominin taxon that exhibits a hitherto unknown combination of primitive (for example, a small brain) and derived morphology (for example, brow ridges).

The ongoing debate about the origins of our genus is part of *H. habilis*'s legacy. In my view, the species is too unlike *H. erectus* to be its immediate ancestor, so a simple, linear model

explaining this stage of human evolution is looking less and less likely. Our ancestors probably evolved in Africa, but the birthplace of our genus could be far from the Great Rift Valley, where most of the fossil evidence has been found. The Leakeys' iconic discoveries at Olduvai Gorge should remind us of how much we don't know, rather than how much we do.

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Source: <https://www.nature.com/articles/508031a>

The third one is called *Ardipithecus ramidus*, thought to be an early human-like female anthropoid 4.4 million years old. But do scientists have an agreement about this fossil, or is it just like its sisters?

Nickname: Ardi

Discovery Date: 1994

Where Lived: Eastern Africa (Middle Awash and Gona, Ethiopia)

When Lived: About 4.4 million years ago

Height: Females: average 3 ft 11 inches (120 centimeters)

Weight: Females: average 110 lbs (50 kg)

Overview:

Ardipithecus ramidus was first reported in 1994; in 2009, scientists announced a partial skeleton, nicknamed 'Ardi'. The foot bones in this skeleton indicate a divergent large toe combined with a rigid foot – it's still unclear what this means concerning bipedal behavior. The pelvis, reconstructed from a crushed specimen, is said to show adaptations that combine tree-climbing and bipedal activity. The discoverers argue that the 'Ardi' skeleton reflects a human-African ape common ancestor that was not chimpanzee-like. A good sample of canine teeth of this species indicates very little difference in size between males and females in this species.

Ardi's fossils were found alongside faunal remains indicating she lived in a wooded environment. This contradicts the open savanna theory for the origin of bipedalism, which states that humans learned to walk upright as climates became drier and environments became more open and grassy.

History of Discovery:

A team led by American paleoanthropologist Tim White discovered the first *Ardipithecus ramidus* fossils in the Middle Awash area of Ethiopia between 1992 and 1994. Since that time, White's team have uncovered over 100 fossil specimens of *Ar. ramidus*. White and his colleagues gave their discovery the name *Ardipithecus ramidus* ('ramid' means 'root' in the Afar language of Ethiopia and refers to the closeness of this new species to the roots of humanity, while 'Ardi' means 'ground' or 'floor'). At the time of this discovery, the genus *Australopithecus* was scientifically well established, so White devised the genus name *Ardipithecus* to distinguish this new genus from *Australopithecus*. In 2009, scientists formally announced and published the findings of a partial skeleton (ARA-VP-6/500), nicknamed "Ardi", first found in 1994.

How They Survived:

Ardipithecus ramidus individuals were most likely omnivores, which means they enjoyed more generalized diet of both plants, meat, and fruit. *Ar. ramidus* did not seem to eat hard, abrasive foods like nuts and tubers.

How do we know they were omnivores?

The enamel on *Ar. ramidus* teeth remains show it was neither very thick nor very thin. If the enamel was thick, it would mean *Ar. ramidus* ate tough, abrasive foods. If the enamel was thin, this would suggest *Ar. ramidus* ate softer foods such as fruit. Instead, *A. ramidus* has an enamel thickness between a chimpanzee's and later *Australopithecus* or *Homo* species, suggesting a mixed diet. However, the wear pattern and incisor sizes indicate *Ar. ramidus* was not a specialized frugivore (fruit-eater). *Ar. ramidus* probably also avoided tough foods, as they did not have the heavy chewing specializations of later *Australopithecus* species.

Evolutionary Tree Information:

Over 100 specimens of *Ardipithecus ramidus* have been recovered in Ethiopia. Even though it has some ape-like features (as do many other early human species), it also has key human features including smaller diamond-shaped canines and some evidence of upright walking. It may have descended from an earlier species of *Ardipithecus* that has been found in the same area of Ethiopia, *Ardipithecus kadabba*.

Questions:

We don't know everything about our early ancestors—but we keep learning more! Paleoanthropologists are constantly in the field, excavating new areas with groundbreaking technology, and continually filling in some of the gaps about our understanding of human evolution.

Below are some of the still unanswered questions about *Ardipithecus ramidus* that may be answered with future discoveries:

1. Does the pelvis of *Ar. ramidus* support the hypothesis that this early human species was bipedal? The pelvis was reconstructed from crushed fossils and, according to some scientists, is only suggestive of bipedalism.
2. What is the average size of male *Ar. ramidus* individuals? If more fossils support the original finding of relatively low sexual dimorphism, how does this relate to male and female size differences in other early humans at the base of our family tree -- and what does it mean?

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ARA-VP-6/500

A partial skeleton of a female, known as "Ardi", combines human and other primate traits. Ardi moved in the trees using a grasping big toe, yet her pelvis was shorter and broader than an ape's, indicating that she could walk bipedally.

Source: <https://humanorigins.si.edu/evidence/human-fossils/species/ardipithecus-ramidus>

Ardi: The Human Ancestor Who Wasn't?

By Eben Harrell Thursday, May 27, 2010



Reuters / Corbis

A reconstructed frontal view of Ardi

At a little over 4 ft. tall, she was small by human standards. But when Ardi, the 4.4 million-year-old hominid fossil found in Ethiopia in 1992, was finally introduced to the world last October in a series of 11 audacious studies in the journal *Science*, she caused big waves in evolutionary circles. Both *TIME* and *Science* named her the "Scientific Breakthrough of the Year." But now Ardi has found herself in a spot of controversy. Two new articles being published by *Science* question some of the major conclusions of Ardi's researchers, including whether this small, strange-looking creature is even a human ancestor at all.

Neither article challenges the veracity of the evidence published by the team of scientists, led by paleoanthropologist Tim White of the University of California, Berkeley, which painstakingly pieced Ardi together from more than 100 crushed fossil fragments. But they do dispute the conclusions White and his colleagues reached from that evidence.

[\(See the top 10 scientific discoveries of 2009.\)](#)

In the first article, titled "Comment on the Paleobiology and Classification of *Ardipithecus ramidus*," Esteban Sarmiento, a primatologist at the Human Evolution Foundation, argues that many of the "characters" — the scientific term for physical traits — used by White to place Ardi on the human lineage are also shared by other primates. He argues that the evidence suggests Ardi belongs to a species that evolved before the moment when humans, apes and chimps diverged along different evolutionary paths. That is significant because one of the things that made Ardi interesting scientifically was that she had been identified by White as the earliest known descendant of the last common ancestor of humans and African apes — thus her physiology could offer clues to what makes humans different from their nearest relatives.

"[White] showed no evidence that Ardi is on the human lineage," Sarmiento says. "Those characters that he posited as relating exclusively to humans also exist in apes and ape fossils that we consider not to be in the human lineage."

[\(See how Ardi was first discovered.\)](#)

The biggest mistake White made, according to the paper, was to use outdated characters and concepts to classify Ardi and to fail to identify anatomical clues that would rule her out as a human ancestor. As an example, Sarmiento says that on the base of Ardi's skull, the inside of the jaw joint surface is open as it is in orangutans and gibbons, and not fused to the rest of the skull as it is in humans and African apes — suggesting that Ardi diverged before this character developed in the common ancestor of humans and apes.

White, no surprise, has defended his analysis, publishing a written response of his own in *Science*. In an e-mail exchange with TIME, he says, "Dr. Sarmiento's views appear to be uniquely his own. Most notable in Dr. Sarmiento's comment is his refusal to recognize as significant the multiple and independently derived features of the *Ardipithecus* cranium, dentition, and postcranial skeleton. These features uniformly align this primate with all later hominids to the exclusion of any other ape — living or fossil. Has Dr. Sarmiento shown how the *Ardipithecus* evidence better fits his interpretation than the one we published? Not here."

But Sarmiento's is not the only attack on White's and his colleagues' work. In a separate comment in *Science*, eight geologists and anthropologists from seven universities question White's conclusion that Ardi lived in a wooded area rather than on open grassland. At the launch of the Ardi papers, White had argued that the wooded terrain Ardi called home disproved the "savanna hypothesis" of bipedalism — the theory that what got our ancestors walking on two legs in the first place was a change in climate that transformed African forest into savanna. In such an environment, goes the reasoning, upright primates would have had the advantage over knuckle walkers because they could see over tall grasses to avoid predators and search for food and carry it back to their homes.

Reached by Internet chat in Kenya, University of Utah geochemist Thure Cerling, lead author of the *Science* critique, accuses the Ardi team of misinterpreting its data. Carbon measures and other studies on the rock around the Ardi site suggest that tropical grasses contributed up to 77% of Ardi's ecosystem, Cerling says. While acknowledging that there was evidence that woodland existed around Ardi as well, Cerling tells TIME that "early humans had available to them, at no great distance, the resources of the savanna and probably those of the riparian woodland as well." The savanna hypothesis, he adds, remains "a viable idea."

[\(See how Neanderthal DNA lives on in modern humans.\)](#)

Responding to the critique, White accuses Cerling and his co-authors of "downplaying and ignoring" evidence of forests around Ardi in order to "accommodate their long-held hypothesis that earliest hominid evolution was savanna-driven." He adds that "we have never claimed that there was no grass in Ardi's world," but rather that early hominids simply had "preferences for — and adaptations to — woodland habitats."

While Sarmiento regards the hype around Ardi to have been overblown, Cerling says he still feels the discovery and re-creation of the ancient specimen to be a monumental breakthrough. But, he says, the science was in the evidence collected by White and colleagues, and not in their conclusions. "Many students will thoroughly examine the data and will come to their own independent evaluations," he says. In other words, science works a bit like evolution, and asking whether Ardi will survive as a major advancement is rather like going into the distant past and asking what the fate of her species would be: Only time will tell.

Source: https://content.time.com/time/health/article/0,8599,1992115,00.html?xid=rss-topstories&fbclid=IwAR0tGl_v7S5S680bjdxrlSU9c26U0ZkF0mgKGhGni78SYZz0mJBaCV3xsAA

Was 'Ardi' really human ancestor?

Last fall, a fossil skeleton named "Ardi" shook up the field of human evolution. Now, some scientists are raising doubts about what exactly the creature from Ethiopia was and what kind of landscape it inhabited.

May 27, 2010, 5:59 PM UTC / Source: The Associated Press

By By Malcolm Ritter

Last fall, a fossil skeleton named "Ardi" shook up the field of human evolution. Now, some scientists are raising doubts about what exactly the creature from Ethiopia was and what kind of landscape it inhabited.

New critiques question whether Ardi really belongs on the human branch of the evolutionary tree, and whether it really lived in woodlands. That second question has implications for theories about what kind of environment spurred early human evolution.

The new work is being published by the journal Science, which last year declared the original presentation of the 4.4 million-year-old fossil to be the magazine's breakthrough of the year.

Ardi, short for *Ardipithecus ramidus*, is a million years older than the famous "Lucy" fossil. Last October, it was hailed as a window on early human evolution.

Researchers concluded that "Ardi" walked upright rather than on its knuckles like chimps, for example, and that it lived in woodlands rather than open grasslands. It didn't look much like today's chimps, our closest living relatives, even though it was closer than Lucy to the common ancestor of humans and chimps.

Such questioning isn't unusual; big scientific discoveries are typically greeted that way. Until more scientists can study the fossil and other work can be done, broad consensus may be elusive. The 2003 discovery of diminutive fossil "hobbits" in Indonesia, for example, has spurred a long-running debate about whether the hobbits were a separate species or not.

Wrong evolutionary tree?

Tim White of the University of California, Berkeley, one of the scientists who described Ardi last year in Science, said he isn't surprised by this week's debate.

"It was completely expected," he said. "Any time you have something that is as different as Ardi, you're probably going to have it."

Esteban Sarmiento of the Human Evolution Foundation in East Brunswick, N.J., wrote in the new analysis that he's not convinced Ardi belongs on the evolutionary tree branch leading to modern humans.

Instead, he said in an interview, he thinks it came along earlier, before that human branch split off from the ancestors of chimps and gorillas.

The specific anatomical features of teeth, the skull and elsewhere that the researchers cited just don't make a convincing case for membership on the human branch, he argued. Some, like certain features in the wrist and where the lower jaw connects to the skull, indicate instead that Ardi arose before humans split off from African apes, he said.

In a written rebuttal in Science and in a telephone interview, White disagreed with Sarmiento's conclusion. "The evidence is very clear that in Ardipithecus, there are characteristics shared only by later hominids ... and humans," White said.

If Ardi were really ancestral to chimps, certain features of its teeth, pelvis, and skull would have had to later evolve back to their more ape-like conditions, an "evolutionary reversal that's highly unlikely," White said in an interview.

Two other experts, however, said in interviews that they think it's too early to tell where Ardi fits on the evolutionary tree.

Will Harcourt-Smith, a research associate at the American Museum of Natural History and member of the anthropology department at Lehman College in New York, said he could not say whether Sarmiento was right or wrong.

Source: <https://www.nbcnews.com/id/wbna37379481>

Today, we are talking about the most famous human ancestor on the evolution tree of the human being, it is the Neanderthal.

Lived from about 400,000 to 40,000 years ago

Brain size: At least 1,200 cubic centimeters

Height: About 1.5-1.75 m

Weight: About 64-82 kg

Diet: Meat, plants and fungi, shellfish when available

Where: Across Europe and southwest and central Asia

Neanderthals were humans like us, but they were a distinct species called *Homo neanderthalensis*. The scientist was thinking that their extinction took place because of their mental inferiority compared to the humans, and assumed that they are just a human ancestor. That is not true, because those assumptions are based upon incomplete data. The reason I'm saying that Neanderthals are humans is that the recent studies prove that there is no mental inferiority in their case because these recent studies prove that Neanderthals were able to make their own tools without the help of any modern humans, and were very good at fishing and hunting, knew how to use fire in their favour. Not just that, they also knew how to trade and were capable of speaking due to studies by using Advanced CT scan, proving that they have similar vocal cords to us, and the same gene responsible for speaking, which is "FOXP2" which is, by the way, different in chimpanzees. That's why they can't speak, but in the case of Neanderthals, the majority of data refers that they are able to speak, and the very significant discovery that I am impressed by was the main reason for considering the Neanderthals humans, is that they had spiritual experiences and religions, and the evidence for that is that some studies proved that some of their fossils prove burying their dead or burning them with very specific, spiritual details.

Neanderthals could talk like humans, study suggests

By

- [Sara Rigby](#)

Published: 02nd March, 2021 at 12:02

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Our cousins' ears were tuned to the frequencies used in human communication.

Humans were thought to have spoken language unlike any other species on Earth. But now, scientists think another species of human, the Neanderthal, had the ability to hear and produce speech just like us.

“For decades, one of the central questions in human evolutionary studies has been whether the human form of communication, spoken language, was also present in any other species of

human ancestor, especially the Neanderthals,” said [Prof Juan Luis Arsuaga](#) at the Universidad Complutense de Madrid, one of the co-authors of the study.

The international team of researchers studied the auditory capacities of Neanderthals, *Homo sapiens* and ancestors to Neanderthals from the archaeological site Atapuerca.

By using high-resolution CT scans, they created virtual 3D models of the ear structures of each species. They used this data to model the frequencies that each species could hear the best.

Though the human ear can hear sounds between frequencies of 20Hz and 20kHz, the majority of human speech sounds are up to 5kHz. Neanderthals showed a greater sensitivity in the frequency range of 4-5 kHz than their ancestors from Atapuerca, similarly to *Homo sapiens*.

The researchers also looked at the ‘occupied bandwidth’ of each species: the range of frequencies to which the ear is most sensitive.

A wider occupied bandwidth means the species can distinguish a wider range of sounds, and so communicate more effectively. Neanderthals’ occupied bandwidth was wider than their ancestors’, and similar to *Homo sapiens*.

The fact that Neanderthals had this hearing fine-tuned to human speech, which hadn’t been evolved by their ancestors in Atapuerca, suggests that they [had the capacity for speech](#) to go alongside it.



3D model and virtual reconstruction of the ear in a modern human (left) and a Neanderthal (right) © Mercedes Conde-Valverde

“The presence of similar hearing abilities, particularly the bandwidth, demonstrates that the Neanderthals possessed a communication system that was as complex and efficient as

modern human speech,” said [Prof Mercedes Conde-Valverde](#) at the Universidad de Alcalá in Spain, lead author of the study.

Neanderthals could even have had a form of language, the researchers believe. However, that doesn't necessarily mean they had the mental faculties to speak the same language as ancient humans.

[Prof Rolf Quam](#), co-author of the study, is confident in the study's findings. “This is one of the most important studies I have been involved in during my career,” he said. “The results are solid and clearly show the Neanderthals had the capacity to perceive and produce human speech.”

Reader Q&A: Why did the Neanderthals go extinct?

Asked by: Kevin Simpson, Durham

The spread of modern humans across Europe is associated with the demise and ultimate extinction of Neanderthal populations 40,000 years ago, likely due to competition for resources.

While the jury is still out on whether or not Neanderthals and modern humans differed in cognition, the ability of a small number of humans to replace a larger population of Neanderthals may have been due to a higher level of culture – our power to develop and pass on knowledge of better tools, better clothing, or better economic organisation.

Interbreeding may also have lent us an advantage. Between 1 and 4 per cent of the DNA of all living humans (except sub-Saharan Africans) is Neanderthal in origin.

Source: <https://www.sciencefocus.com/news/neanderthals-could-talk-like-humans-study-suggests/>

Neanderthals were able to 'develop their own tools'

- Published
- 24 September 2010



Image caption,
It is still unknown why Neanderthals went extinct
By Katia Moskvitch
Science reporter, BBC News

Neanderthals were keen on innovation and technology and developed tools all on their own, scientists say.

A new study challenges the view that our close relatives could advance only through contact with *Homo sapiens*.

The team says climate change was partly responsible for forcing Neanderthals to innovate in order to survive.

The research is set to appear in the Journal of Archaeological Method and Theory in December.

"Basically, I am rehabilitating Neanderthals," said Julien Riel-Salvatore, assistant professor of anthropology at the University of Colorado in Denver, who led the seven-year study.

"They were far more resourceful than we have given them credit for."

Vanished culture

Neanderthals were first discovered in Germany's Neander Valley in 1856.

It is believed that they lived in Europe and parts of Asia. Close examination of the found fossils shows that they shared 99.5-99.9% of modern humans' DNA, which makes them our closest relatives.

They had short, muscular bodies, large brains, prominent facial features and barrel chests.

Neanderthals split from our evolutionary line some 500,000 years ago, and disappeared off the face of the Earth about 30,000 years ago.

Since the first discovery, anthropologists have been trying to crack the mystery of the vanished culture, also debating whether or not Neanderthals were evolving on their own or through contact with *Homo sapiens*.

During the research, Dr Riel-Salvatore and his colleagues examined Neanderthal sites across Italy.

About 42,000 years ago, *Homo sapiens* and Neanderthals were already living in the northern and central parts of the area.

At that time, an entirely new group appeared in the south.

The researchers believe that the southerners were also Neanderthals, of a culture named Uluzzian.

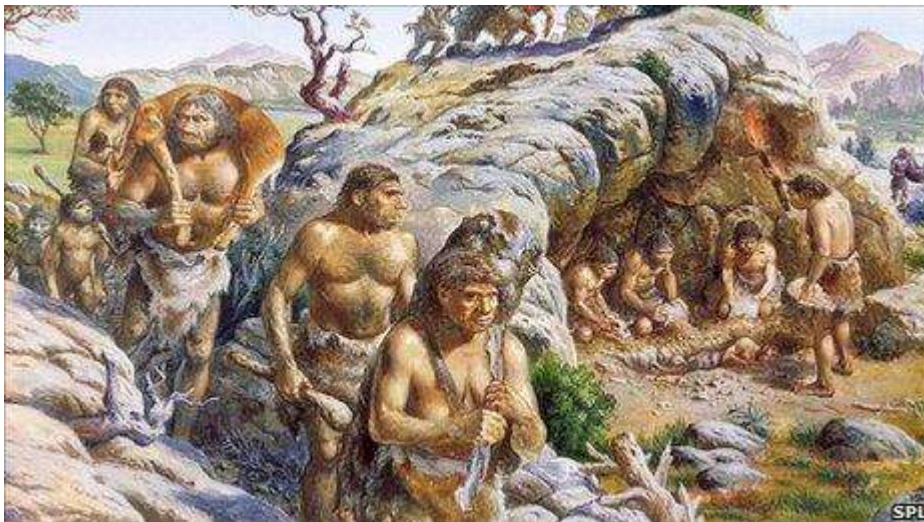


Image caption,
Neanderthals lived in Europe and parts of Asia

Dr Riel-Salvatore's team was astonished to find quite a few innovations throughout the area, even though the Uluzzians were isolated from *Homo sapiens*.

They discovered projectile points, ochre, bone tools, ornaments and possible evidence of fishing and small game hunting.

"My conclusion is that if the Uluzzian is a Neanderthal culture, it suggests that contacts with modern humans are not necessary to explain the origin of this new behaviour.

"This stands in contrast to the ideas of the past 50 years that Neanderthals had to be acculturated to [modern] humans to come up with this technology.

"When we show Neanderthals could innovate on their own, it casts them in a new light.

"It 'humanises' them, if you will."

Brothers?

The researchers believe that one reason that forced Neanderthals to innovate was a shift in climate.

When the area where they were living started to become increasingly open and arid, they had no choice but to adapt - or die out.

"The fact that Neanderthals could adapt to new conditions and innovate shows they are culturally similar to us," said Dr Riel-Salvatore.

He added that they were also similar biologically, and should be considered a subspecies of human rather than a different species.

"My research suggests that they were a different kind of human, but humans nonetheless.

"We are more brothers than distant cousins."

Source: <https://www.bbc.com/news/science-environment-11408298>

Neanderthals Turned to Faith When Confronting Death, New Evidence Suggests

We aren't sure whether they could speak, let alone intone liturgy over their dead in the light of controlled fires, but a child's burial site in Spain suggests they might well have, say archaeologists.

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[Ruth Schuster](#)

Dec 15, 2016

The recent discovery of possible elaborate funeral rites by Neanderthal cavemen has begged the question of whether these primitive cousins of Man had religion. Not to mention, whether they could control fire.

- [Ancient Men in Israel Ate Elephants](#)
- [Second Temple Courtyard Flooring Restored](#)
- [4,000-year Old Version of 'The Thinker' Found in Israel](#)

The latest discovery suggesting that Neanderthals were not beetle-browed brutes is the seemingly intentional burial of a child about 40,000 years ago, in a cave some 100 kilometers from Madrid. The burial site of the so-called [Loyozza Child](#) was surrounded by hearths, in each of which the archaeologists found bones, antlers and nearby, one rhino skull. The child itself had been two to three years old and seems to have had its body burned. The team feels the fires could have been ceremonial rather than functional.

The fire for the child's body and hearths could have been collected serendipitously, for instance, from bushfires created by lightning, as primitive hominins did for hundreds of thousands of years at least. (Where and when [primitive man learned to control fire](#), as opposed to merely taking advantage of it, remains hotly contested.) The bones could be the remains of animals who had been cooked on the fires and eaten. And, like today's teenagers, Neanderthals could have been the sort of slob who leave the bones in the cave.

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Or the cave dwellers may have had [elaborate mortuary rites](#), which could indicate that they cherished their dead, which could in turn indicate spiritual depths.

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While researchers disagree about Neanderthal use of fire in Europe, here in the Levant, researchers have long been convinced that Neanderthals used it regularly, Prof. Erella Hovers of the Hebrew University of Jerusalem told Haaretz. "On this the archaeological evidence in Israel and Syria is categorical," she wrote by email.

They also believe that, like primitive humans, at least some of the Neanderthals buried their dead some of the time, with intentionality, an inference based on the positioning of bodies, seeming funerary offerings and more, Hovers adds. (She also points out that there's no suggestion that every Homo sapiens from the middle Paleolithic, between 100,000 and 40,000 years ago, was intentionally buried by mourning kinfolk). She also points out that the proof the child in question was in fact Neanderthal remains outstanding.

Not necessarily a sentimental bunch

Its Neanderthal identification being as it may, the Loyoza Child is not the only postulated Neanderthal funeral. In 2013, archaeologists reported on evidence of a [Neanderthal burial in at the site of La Chapelle-aux-Saints](#) in France. Whether the French Neanderthal was intentionally buried there is another question, but the archaeologists felt the evidence showed that he was. Another [Neanderthal child was found in a cave in Roc de Marsal](#), Dordogne, from about 70,000 years ago, and was postulated to be a deliberate burial.

In Israel, in 1992 the [articulated partial skeleton of a Neanderthal infant](#) was excavated, in Amud Cave: based on its state of protection and preservation versus that of other faunal remains in the cave, the archaeologists concluded it had been purposefully buried.

"Assuming it was Neanderthal, I think I have to agree with [the researching archaeologist] Chris Stringer, that the discovery demonstrates much more complex behavior than had been documented until today in Neanderthal burials," Hovers sums up.



Remains of Neanderthal child, believed to be about 3 years old, found in Roc de Marsal: Also believed to have been ceremoniously interred. Credit: Don Hitchcock 2014, Wikimedia Commons

If so, the Neanderthal had the capacity to recognize death and mark it, as opposed for instance to leaving the body where it lay for scavengers to eat. Or to eat themselves. At least some Neanderthals [did not cavil at cannibalism](#), for example going by evidence found in Belgium. At yet other sites, there is evidence that Neanderthals unromantically used the bones of their dead to sharpen their stone tools.

Just how sophisticated were they, the Neanderthals?

In practice, we don't even know if they could speak. Recent excavations have discovered that the [Neanderthals had hyoid \(tongue\) bones like humans](#). "In my opinion, that hyoid bone isn't what will tell us if they spoke or not," cautions Prof. Yoel Rak of Tel Aviv University, expert on Neanderthal anatomy. "That is, the Neanderthal bone is very different from that of the chimp and very much like ours. But based on to similarity— they could speak."

Certainly, we know that the Neanderthal brain was as big as ours or even bigger, Rak adds. And crucially, Neanderthals had the right gene for speech, FOXP2, just like we do. Chimpanzees for instance have FOXP2 but it differs from the human version.

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Intriguingly, Rak points out, humans born with "pathological" FOXP2 can't understand speech. "To cut to the chase, we and the Neanderthals have exactly the same gene without the pathology. This could lead us to conclude that they could speak," he happily speculates.

Even if they didn't, they could have communicated in any number of ways, he points out. "We can also speak in sign language. Even *Homo sapiens* has for instance click languages where communication is effected but not through the voice box. Or there are whistles," Rak says.

Ergo, he sums up, the ability to communicate and to exchange thoughts is intellectual, not anatomic.

Another sign of sophistication could be art. But the general consensus over "Neanderthal art" is that there was none.

The one possible sign of Neanderthals being abstractly artistic is a 55,000-year old flute made out of a young cave bear's bone found in 1995 in Slovenia, says Rak. (He's not a great believer in the famous cross-hatched "[Neanderthal engraving](#)" in Gibraltar.)

Some believe it [wasn't musically minded prehistoric men who made the holes in the flute, but hyenas](#). Yet others point out that [the bone flute makes beautiful music](#), which hyenas don't care about.



A Neanderthal flute, or a hyena's chew toy? Credit: Wikimedia Commons

Speaking of tools, another relevant argument in archaeological circles is who taught who to use lissoirs, tools still used today in leather working. Archaeologists thought Man invented the lissoir and that Neanderthals poached the idea shortly before going extinct. But in 2013, archaeologists working in Grosse Grotte, Germany discovered lissoirs in a Neanderthal context preceding the time when humans supplanted their thicker-bodied cousins. They are the [oldest-known specialized bone tools in Europe](#) and indicate that the Neanderthals invented them and we were the ones who borrowed the idea.

Spirituality on and in my mind

So maybe they could speak and play music; paintings are unknown; but did they have spirituality? Could they have believed in God? gods? The morrow, or even an afterlife?

When Homo sapiens began believing in deities is not known. Some think that a rock with carved bits looking very, very vaguely like a large snake, found in a Botswana cave, [depicts a god worshipped by the predecessors of the Sana people 70,000 years ago](#). Evidence of ritualistic behavior at the site includes spearheads that seem to have been deliberately burned or broken, which would be an odd thing to do without a ritualistic context.

The prehistoric Botswanans may well have been predisposed to believe in a python god or divine porcupine or whatever. So may Neanderthals. A predisposition to believe seems to be hard-wired into *homo* brains.

The neurological basis theory has been making the rounds since at least 2008, based on brain scans of praying people and the observation that social activity, like burning pagans together or going to synagogue, leads to the release of feel-good juice, a.k.a., serotonin. Worship, with or without ecstasy, is a relatively low-energy way to produce that serotonin that we crave. And, our brain biochemistry receives backing from none other than our egos: the world was created for us!

Faith might also arise from our brains resorting to illogic to find "order" in the dismaying chaos around us. We like order. Neanderthals may have too.

Some psychologists insist faith is pathological, in that it involves irrationality and even malignancy: just think of the mass murders in the name of religion. Who knows, maybe it's even how Neanderthals, some of them, some of the time, wound up eating their dead.

Source: <https://www.haaretz.com/archaeology/2016-12-15/ty-article/did-neanderthals-believe-in-god/0000017f-deea-d3a5-af7f-feeec3e70000>

Relationship to *Homo sapiens*

The question of ancestry

A few researchers have generally opposed the view that *H. erectus* was the direct ancestor of later [species](#), including *Homo sapiens*. [Louis Leakey](#) argued energetically that *H. erectus* populations, particularly in Africa, overlap in time with more advanced *Homo sapiens* and therefore cannot be ancestral to the latter. Some support for Leakey's point of view has come from analysis of anatomic [characteristics](#) exhibited by the fossils. By emphasizing a distinction between "primitive" and "derived" traits in the reconstruction of relationships between species, several paleontologists have attempted to show that *H. erectus* does not make a suitable morphological ancestor for *Homo sapiens*. Because the braincase is long, low, and thick-walled and presents a strong browridge, they claim that *H. erectus* shows derived (or specialized) characteristics not shared with more modern humans. At the same time, it is noted, *Homo sapiens* does share some features, including a rounded, lightly built cranium, with earlier hominins such as *H. habilis*. For these reasons, some paleontologists (including Leakey) consider the more slender, or "gracile," *H. habilis* and *H. rudolfensis* to be more closely related to *Homo sapiens* than is *H. erectus*. These findings are not widely accepted, however. Instead, studies of size in human evolution indicate that representatives of *Homo* can be grouped into a reasonable ancestor-to-descendant sequence showing increases in body size. Despite having a heavier, more flattened braincase, *H. erectus*, most particularly the African representatives of the species sometimes called *H. ergaster*, is not out of place in this sequence.

If this much is agreed, there is still uncertainty as to how and where *H. erectus* eventually gave rise to *Homo sapiens*. This is a major question in the study of human evolution and one that resists resolution even when [hominin](#) fossils from throughout the Old World are surveyed in detail. Several general [hypotheses](#) have been advanced, but there is still no firm [consensus](#) regarding models of gradual change as opposed to scenarios of rapid evolution in which change in one region is followed by migration of the new populations into other areas.

Theories of gradual change

A traditional view held by some paleontologists is that a species may be transformed gradually into a succeeding species. Such successive species in the evolutionary sequence are called chronospecies. The boundaries between chronospecies are almost impossible to determine by means of any objective anatomic or functional criteria; thus, all that is left is the guesswork of drawing a boundary at a moment in time. Such a chronological boundary may have to be drawn arbitrarily between the last survivors of *H. erectus* and the earliest members of a succeeding species (e.g., *Homo sapiens*). The problem of defining the limits of chronospecies is not peculiar to *H. erectus*; it is one of the most vexing questions in paleontology.

Such gradual change with [continuity](#) between successive forms has been postulated particularly for [North Africa](#), where *H. erectus* at [Tighenif](#) is seen as ancestral to later populations at Rabat, Temara, Jebel Irhoud, and elsewhere. Gradualism has also been postulated for [Southeast Asia](#), where *H. erectus* at Sangiran may have progressed toward populations such as those at Ngandong (Solo) and at Kow Swamp in Australia. Some

researchers have suggested that similar developments could have occurred in other parts of the world.

The supposed interrelation of cultural achievement and the shape and size of teeth, jaws, and brain is a theorized state of affairs with which some paleoanthropologists disagree. Throughout the human [fossil record](#) there are examples of dissociation between skull shape and size on the one hand and cultural achievement on the other. For example, a smaller-brained *H. erectus* may have been among the first humans to tame fire, but much bigger-brained people in other regions of the world living later in time have left no evidence that they knew how to handle it. Gradualism is at the core of the so-called “[multiregional hypothesis](#)” (see [human evolution](#)), in which it is theorized that *H. erectus* evolved into *Homo sapiens* not once but several times as each subspecies of *H. erectus*, living in its own territory, passed some postulated critical [threshold](#). This theory depends on accepting a supposed *erectus-sapiens* threshold as correct. It is opposed by supporters of the “[out of Africa](#)” hypothesis, who find the threshold concept at variance with the modern genetic theory of evolutionary change.

Theories of [punctuated change](#)

A gradual transition from *H. erectus* to *Homo sapiens* is one interpretation of the fossil record, but the evidence also can be read differently. Many researchers have come to accept what can be termed a punctuated view of human evolution. This view suggests that species such as *H. erectus* may have exhibited little or no morphological change over long periods of time (evolutionary stasis) and that the transition from one species to a descendant form may have occurred relatively rapidly and in a restricted geographic area rather than on a worldwide basis. Whether any *Homo* species, including our own, evolved gradually or rapidly has not been settled.

The continuation of such arguments underlines the need for more fossils to establish the range of physical variation of *H. erectus* and also for more discoveries in good archaeological [contexts](#) to permit more precise dating. Additions to these two bodies of data may settle remaining questions and bring the problems surrounding the evolution of *H. erectus* nearer to resolution.

[Phillip Vallentine Tobias](#)[G. Philip Rightmire](#)

Source: <https://www.britannica.com/topic/Homo-erectus/Relationship-to-Homo-sapiens>

And finally, the biggest paper about the Neanderthals, which discussed 151 different studies about them and proved that the reason for their disappearance is not because they couldn't compete with modern humans due to inferiority, but instead the only reason is that Neanderthals merge together with humans and were able to have families, and their DNA is still present in the modern humans with similarity of about 99.9%.

Neandertal Demise: An Archaeological Analysis of the Modern Human Superiority Complex

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Abstract

Neandertals are the best-studied of all extinct hominins, with a rich fossil record sampling hundreds of individuals, roughly dating from between 350,000 and 40,000 years ago. Their distinct fossil remains have been retrieved from Portugal in the west to the Altai area in central Asia in the east and from below the waters of the North Sea in the north to a series of caves in Israel in the south. Having thrived in Eurasia for more than 300,000 years, Neandertals vanished from the record around 40,000 years ago, when modern humans entered Europe. Modern humans are usually seen as superior in a wide range of domains, including weaponry and subsistence strategies, which would have led to the demise of Neandertals. This systematic review of the archaeological records of Neandertals and their modern human contemporaries finds no support for such interpretations, **as the Neandertal archaeological record is not different enough to explain the demise in terms of inferiority in archaeologically visible domains.** Instead, current genetic data suggest that complex processes of interbreeding and assimilation may have been responsible for the disappearance of the specific Neandertal morphology from the fossil record.

Figures

1. AMH had "complex symbolic communication systems" and "fully syntactic language", while Neandertals did not.
2. Neandertals had limited capacity for innovations.
3. Neandertals were less efficient hunters.
4. Neandertal weaponry was inferior to AMH projectile technology.
5. Neandertals had a narrower diet, unsuccessful in competition with AMH with their more diverse diets.
6. The use of traps and snares to capture animals was the exclusive domain of AMH.
7. AMH had larger social networks.
8. The total AMH populations entering Neandertal territory were significantly larger than regional Neandertal populations.
9. Hunting by AMH required complex procedures indicative of modern cognition, while Neandertals hunting was a simple procedure using naturally available game.
10. Cold climate around 40 ka was a factor in Neandertal decline.
11. Expansion of Mount Tiber volcanic at 73 ka played an indirect role in Neandertal extinction.
(a) See Text S1 Hypotheses 1-11 for details. doi:10.1371/journal.pone.0264244.g001

Technological phase	Start (ka)	End (ka)
Skill Set		
Bombus	ca 75.5 (55%)	47.8 (55%)
Shufu	70.3-62.0 (55%)	
Chickadee	100-110 (55%)	
Neolithic Phase		
Shufu	64.7-5.5 (55%)	45.7-2.2 (55%)
Klaus River Main Site, Cave 1A	64.7-5.5 (55%)	50-3 (55%)
Bombus Cave	74-4 (55%)	40-3 (55%)
Chickadee	100-110 (55%)	52.5-19 (55%)
Post-Neolithic Phase (MSA II)		
Klaus, Cave 1A	60-3 (55%)	-
Klaus, Cave 1B	57.9-5.5 (55%)	-
Bombus Cave	60-3 (55%)	40-42 (7% C-14 BP)
Shufu	58.3-1.4 (55%)	38.8-1.9 (55%)
Bombus	ca 56-16 (55%)	38-36 (7% C-14 BP)
Klaus, Cave 1A	57.8-1.4 (55%)	33.3-1.8 (55%)
Klaus, Cave 1B	56.0-3.9 (55%)	-
Neolithic in Western Europe (1)		
Neolithic of Atlantic Tradition	70	40
Old World in SW France	75	40
Quina Mousterien	75	40
Old World in SW France	75	40
The Atlantic Mousterien	80	50
(1) AMH (80-11-12, 14, 16-18). We have excluded assemblages with uncertain stratigraphy (Simonsen, HP layers at Klein Kichu) or unpublished dates (Hollis Rock, Havel).		
(2) The term Post-Neolithic Phase is equivalent to MSA II at Klaus River Main Site. It includes informal designations of the Sibudu sequence such as late MSA and final MSA. We have not included several TS and US dates for the HP and Post-HP of Kwa Cragge because they are inconsistent or only informative for the middle part of the sequence (215-100). The Post-HP US date reported here for Kwa Cragge (80) is of type LH which is toward the base of the Post-HP sequence but above its oldest layer.		
(3) The Middle Paleolithic technocomplexes are dated by TL, ESR, ¹⁴ C calibrated BP and chronopotigraphy.		
doi:10.1371/journal.pone.0264244.g002		

1. AMH had "complex symbolic communication systems" and "fully syntactic language", while Neandertals did not.
2. Neandertals had limited capacity for innovations.
3. Neandertals were less efficient hunters.
4. Neandertal weaponry was inferior to AMH projectile technology.
5. Neandertals had a narrower diet, unsuccessful in competition with AMH with their more diverse diets.
6. The use of traps and snares to capture animals was the exclusive domain of AMH.
7. AMH had larger social networks.
8. The total AMH populations entering Neandertal territory were significantly larger than regional Neandertal populations.
9. Hunting by AMH required complex procedures indicative of modern cognition, while Neandertals hunting was a simple procedure using naturally available game.
10. Cold climate around 40 ka was a factor in Neandertal decline.
11. Expansion of Mount Tiber volcanic at 73 ka played an indirect role in Neandertal extinction.
(a) See Text S1 Hypotheses 1-11 for details. doi:10.1371/journal.pone.0264244.g001

Technological phases	Start (ka)	End (ka)
Saït Bay		
Bombula	~9.75.5 (25k)	47.8 (25k)
Shubia	30.5-23.0 (56k)	
Diapitof	199-19 (7k)	
Neanderthal Point		
Shubia	94.7-1.5 (25k)	41.7-1.2 (25k)
Klares River Main Site, Core 1A	94.3-2.5 (25k)	36.0-3 (7k)
Bender Cave	74-4 (25k)	40-3 (25k)
Diapitof	199-19 (7k)	32.9-1.9 (7k)
Post-Neanderthal Point/MSA #1		
Klares, Core 1A	40-3 (7k)	—
Klares, Core 1A	17.0-1.3 (25k)	—
Bender Cave	40-3 (25k)	44-42 (7k-6k BP)
Shubia	18.3-1.4 (25k)	38.0-1.9 (25k)
Bombula	~9.75.5 (25k)	38-36 (7k-6k BP)
Klein Kliphuis	17.8-1.4 (25k)	33.3-1.3 (25k)
Rose Cottage	36.0-3.3 (25k)	—
Mousterian in Western Europe (1)		
Mousterian of Acheulian Tradition (in sites in SW France)	70	40
Grotte Mousterien (in sites in SW France)	73	40
The Acheulian (in sites in Germany, Poland and the Czech Republic)	80	50

(1) After [38,39–42,54,56–105], We have excluded assemblages with uncertain stratigraphy (Ambrona, NP layers at Klein Kliphuis) or unpublished dates (Hollase Rock (Switzerland)).

(2) The term Post-Neanderthal Point is equivalent to MSA II at Klares River Main Site. It includes informal designations of the Shubia sequence such as late MSA and Final MSA. We have not included several TL and OSL dates for the NP and Post-NP of Rose Cottage because they are inconsistent or only informative for the middle part of the sequence (205–190). The Post-NP OSL date reported here for Rose Cottage (39) is of layer LN which is toward the base of the Post-NP sequence but above its oldest layer.

(3) The Middle Palaeolithic technocomplexes are dated by TL, ESR, ¹⁴C (calibrated BP) and chronopotigraphy.

doi:10.1371/journal.pone.0096424.t002

1. AMH had "complex symbolic communication systems" and "fully syntactic language", while Neanderthals did not.
2. Neanderthals had limited capacity for innovations.
3. Neanderthals were less efficient hunters.
4. Neanderthal technology was inferior to AMH projectile technology.
5. Neanderthals had a larger diet, unsuccessful in competition with AMH with their more diverse diets.
6. The use of traps and snares to capture animals was the exclusive domain of AMH.
7. AMH had larger social networks.
8. The initial AMH populations entering Neanderthal territory were significantly larger than regional Neanderthal populations.
9. Hunting by AMH required complex procedures indicative of modern cognition, while Neanderthals hunting was a simple procedure using naturally available game.
10. Cold climate around 40 ka was a factor in Neanderthal decline.
11. Expansion of Mount Tiber volcano at 75 ka played an indirect role in Neanderthal extinction.

(a) See Text S1 Hypotheses 1–11 for details.

doi:10.1371/journal.pone.0096424.t001

Technological phases	Start (ka)	End (ka)
Saït Bay		
Bombula	~9.75.5 (25k)	47.8 (25k)
Shubia	30.5-23.0 (56k)	
Diapitof	199-19 (7k)	
Neanderthal Point		
Shubia	94.7-1.5 (25k)	41.7-1.2 (25k)
Klares River Main Site, Core 1A	94.3-2.5 (25k)	36.0-3 (7k)
Bender Cave	74-4 (25k)	40-3 (25k)
Diapitof	199-19 (7k)	32.9-1.9 (7k)
Post-Neanderthal Point/MSA #1		
Klares, Core 1A	40-3 (7k)	—
Klares, Core 1A	17.0-1.3 (25k)	—
Bender Cave	40-3 (25k)	44-42 (7k-6k BP)
Shubia	18.3-1.4 (25k)	38.0-1.9 (25k)
Bombula	~9.75.5 (25k)	38-36 (7k-6k BP)
Klein Kliphuis	17.8-1.4 (25k)	33.3-1.3 (25k)
Rose Cottage	36.0-3.3 (25k)	—
Mousterian in Western Europe (1)		
Mousterian of Acheulian Tradition (in sites in SW France)	70	40
Grotte Mousterien (in sites in SW France)	73	40
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(2) The term Post-Neanderthal Point is equivalent to MSA II at Klares River Main Site. It includes informal designations of the Shubia sequence such as late MSA and Final MSA. We have not included several TL and OSL dates for the NP and Post-NP of Rose Cottage because they are inconsistent or only informative for the middle part of the sequence (205–190). The Post-NP OSL date reported here for Rose Cottage (39) is of layer LN which is toward the base of the Post-NP sequence but above its oldest layer.

(3) The Middle Palaeolithic technocomplexes are dated by TL, ESR, ¹⁴C (calibrated BP) and chronopotigraphy.

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Introduction

The demise of Neandertals is one of the most debated issues in paleoanthropology. Their disappearance in the fossil record constitutes the biological part of a process of change that occurred in Europe and in the Near East between approximately 45 and 35 thousand years ago (ka) [1]–[2]. In western Eurasia, the process led to the replacement of an archaic population (Neandertals) with Middle Paleolithic technologies by a population of modern humans (*Homo sapiens*) with Upper Paleolithic ones [3]–[5]. The study of this process of transition integrates data and scientists from a wide range of disciplines, including archaeologists, physical anthropologists, dating specialists, and increasingly so, geneticists.

Into the 1980's many paleoanthropologists argued that the Neandertals had evolved into modern humans (or modern Europeans) and that the Upper Paleolithic derived from the Middle Paleolithic Neandertal culture. The opposite view assumed a single origin of modern humans and replacement of archaic populations, including Neandertals, by modern humans immigrating from an unknown source area [6]. This view became widely accepted with advances in genetic studies and dating of fossils and sites in Africa, Europe and the Near East. In 1987 the work of Cann and colleagues [7] provided compelling mitochondrial evidence for a recent African origin of all modern humans. Later, the genetic evidence was supported by fossils which showed that Africans were far more modern looking than their Neandertal contemporaries, with dates for the Omo Kibish 1 and Herto skulls in Ethiopia suggesting that the early modern human morphology emerged in East Africa possibly as early as 195,000 year ago [8]–[10]. There is now general agreement that modern humans originated in Africa, and subsequently expanded their range into the Near East and later into Europe. This is the core of the so-called Out-of-Africa hypothesis [11].

In tandem with these developments, archaeologists began looking for modern behavioral markers in African sites dated between 200,000 and 60,000 years ago. Many (see below) would now suggest that there is indeed evidence for significant behavioral and cognitive differences between Neandertals and their African contemporaries, and that when early moderns encountered Neandertals in Western Eurasia, these differences would have entailed the demise of the Neandertals.

Hypotheses for the Demise of Neandertals

Virtually all explanations for the disappearance of the Neandertals from the Eurasian record point in one way or another to the arrival of *Homo sapiens*, anatomically modern humans (AMH), in Europe and western Asia. Late Pleistocene dispersal events brought AMH into the ranges of other hominin populations outside of Africa. In recent years we have seen a series of publications with detailed maps purported to show the progress of modern humans and their new technology across various Eurasian landscapes populated by “archaic” hominins, including Neandertals [12]–[15]. The source populations [16]–[19] and the routes supposedly

taken by the advancing modern humans vary widely in these papers though, as do the chronologies for the supposed Out of Africa dispersal(s) of modern humans. Some archaeological estimates hypothesize an age of around 125 ka for the first AMH dispersals into the Arabian peninsula [20] and around 77 ka for India [21], while others suggest that AMH dispersal, thought to be associated with distinctively African technologies analogous to the “Howiesons Poort”, occurred only around 50–60 ka, i.e. after the Toba volcanic eruption at around 75 ka [22]. Genetic dates for the Out-of-Africa dispersal(s) of AMH also vary widely, between approximately 45 to 130 ka [23]–[25].

The disappearance of the archaic populations, including Neandertals, is routinely explained in terms of the “superiority” of modern humans, who had developed in Africa the ability to evolve complex cultural traditions and had become equipped with cognitive capacities which allowed them to expand globally and replace all other hominins [26], [27]. Such interpretations have increasingly become based on proxies in the Middle Stone Age (MSA) archaeological record of sub-Saharan Africa which, compared to the Middle Paleolithic record of Europe and western Asia, would testify to superiority in a wide range of domains, either in Africa and/or upon arrival of *Homo sapiens* in the Neandertal geographical ranges. These include inventiveness and capacity for innovation [11], [28], complex symbolic and linguistic abilities [29], [30], more efficient hunting strategies [31], exploitation of a broader range of resources including plants and aquatic ones [32], projectile technology [33]–[35], heat treatment of lithic raw materials [36], hafting technology [37], [38], planning capacities including larger scale social networks as shown by large transport distances of raw materials [39], environmental flexibility [40], memory capacity [41] as well as larger population sizes [42]. Inferiority in one or more of these domains has been at the core of many explanations for the demise of the Neandertals.

Prior to the last decade the cultural attributes listed above were generally considered as exclusive manifestations of the western Eurasian Upper Paleolithic, as the result of a major behavioral revolution compared to the preceding Middle Paleolithic. Seen from a European or Near Eastern perspective, the Upper Paleolithic witnessed the introduction of new technologies, the ability to communicate symbolically, systematic use of body ornaments and various forms of mobile and rock art, by modern humans expanding from Africa into Eurasia, leading to the gradual replacement of non-modern populations, such as the Neandertals [29], [43]–[45]. It was acknowledged that some of those features had emerged earlier in Africa, but the most complex technologies and art forms were seen as characteristic of the European Upper Paleolithic, thus clouding the issue of the source area where these innovations had taken place.

In 2000 McBrearty and Brooks [27] forcefully argued that the components of this “Upper Paleolithic revolution” were already visible in the African MSA, tens of thousands of year earlier. They suggested a gradual assembling of a package of modern human behavior in Africa, which was later exported to other regions of the Old World: a view contested by Klein [11], who stressed a later and punctuated emergence of “modern human behavior”. In 2003 D’Errico [46] reviewed the cultural attributes which McBrearty and Brooks saw as defining modernity. He argued that comparable traits also occur in the Neandertal record and rejected the theory that behavioral “modernity” indicators are uniquely associated with *Homo sapiens*. Nevertheless, the behavioral markers described by McBrearty and Brooks have in recent years increasingly been used to explain the demise of the Neandertals when modern humans expanded into their territories.

Non-archaeological data have also been called upon to explain the outcompeting of the large-bodied and big-brained Neandertals by modern humans, but these fall in first instance out of the scope of this review (but see Discussion). The goal of this paper is to test the strength of the archaeology-derived hypotheses for Neandertal extinction referred to above. While some of these hypotheses have been evaluated individually [47], ours is the first systematic study of a wide range explanations. It is timely too, given the large amount of new data generated by fieldwork in Africa, the resulting speculations on modern humans cognitive modernity [28], [30], and new insights into Neandertal behavior and biology, including their biological affinity with modern humans. Genetic studies now suggest that the debate on the demise of the Neandertals needs to be reframed in terms of some degree of interbreeding [23], [48], [49]. In that sense, Neandertals did not go extinct, even though their distinctive morphology did disappear. We will return to this topic at the end of this paper.

Methods

Our evaluation of the key archaeology-derived explanations for the demise of the Neandertals entails a comparative study of the archaeological record of Neandertals and contemporary modern humans, i.e. AMH in Africa and Southwest Asia between 200 and 40 ka. To include younger periods would disregard the effects of cultural and technological evolution after the demise of the Neandertals. The various competing models regarding the evolutionary disadvantages of Neandertals are listed in Table 1 and are reviewed in detail in (Text S1 Hypotheses 1–11), where they are systematically described listing the specific hypothesis and supporting as well as refuting evidence.

1. AMH had "complex symbolic communication systems" and "fully syntactic language", while Neandertals did not.
2. Neandertals had limited capacity for innovation.
3. Neandertals were less efficient hunters.
4. Neandertal technology was inferior to AMH projectile technology.
5. Neandertals had a narrower diet, unsuccessful in competition with AMH with their more diverse diets.
6. The use of traps and snares to capture animals was the exclusive domain of AMH.
7. AMH had larger social networks.
8. The initial AMH populations entering Neandertal territory were significantly larger than regional Neandertal populations.
9. Hunting by AMH required complex procedures indicative of modern cognition, while Neandertal hunting was a simple procedure using naturally available glues.
10. Cold climate around 40 ka was a factor in Neandertal decline.
11. Eruption of Mount Toba volcano at 73 ka played an indirect role in Neandertal extinction.

Table 1. Hypotheses for the demise of Neandertals (a).

<https://doi.org/10.1371/journal.pone.0096424.t001>

Transitional Industries

The so-called “transitional industries”, which show some similarities to late Middle Paleolithic (Mousterian) industries but also contain Upper Paleolithic forms and whose time range falls within a 45–35 ka interval, will not be discussed in detail here, for the following reasons:

1. the makers of the Bohunician, Bachokirian, Szeletian and Streletskayan [in Central and Southeastern Europe and Russia) are not known yet (late Neandertals or AMH?) and hence their status is ambiguous [50].
2. Neandertals are accepted by many—though not by all [51] - as the makers of the Châtelperronian, best known from the Grotte du Renne at Arcy-sur-Cure in France, excavated by Leroi-Gourhan and his team between 1949 and 1963 [52]. The interpretation of the industry, rich in distinctively “modern” cultural features such as ornaments and bone

tools, has been the subject of heated debates. The controversies about whether the ornaments and bone tools were (i) an invention of Neandertals [46], [53], (ii) the result of stratigraphic admixture of Neandertal remains and Upper Paleolithic artifacts [54]–[57], or (iii) due to acculturation [28], [58], [59] have been going on since the acculturation hypothesis was most explicitly discussed in 1998 by D’Errico *et al.* [60]. The stratigraphic integrity of the Châtelperronian layers at the site has been reaffirmed in a recent paper [61], contra [62]. New radiocarbon dates of 44,970–44,520 cal BP for the start and 41,300–40,570 cal BP for the end of the Châtelperronian at Arcy and of 41,950–40,660 cal BP (all dates with probability at 68.2%) for the Saint Césaire Neandertal suggest that the makers of the Châtelperronian ornaments were indeed Neandertals [63]. However, the conflicting hypotheses of acculturation versus independent invention persist, as the dates appear to postdate or overlap in time with the arrival of early modern humans in Italy [5] and with dates for the Aurignacian in Germany [63; contra 2].

Early descriptions of Châtelperronian assemblages stressed a Mousterian component but the industry is now considered Upper Paleolithic in technology, although different from the Aurignacian, and the presence of Mousterian tools as due to syn-or post-depositional mixing [51]. The Châtelperronian lithic industry recently studied at the open-air site Canaule II in France [64] is also described as fully Upper Paleolithic, based on its technology and almost exclusive production of blades and backed points. In contrast to the Arcy site, the very large assemblage of Canaule II comes from a thin and unique layer, with its integrity and homogeneity confirmed by refitting. The absence of any Middle Paleolithic elements in this Châtelperronian assemblage again strongly suggests that the Châtelperronian, chronologically intermediate between the Middle and the Upper Paleolithic, is a unique entity, not the result of a mix of Middle and Upper Paleolithic artifacts.

1. The Uluzzian, an Italian transitional industry also present in Greece and previously attributed to Neandertals [60], [65], is now seen by some as a product of modern humans, on the basis of a study of two deciduous teeth from Grotta del Cavallo in southern Italy [5]. AMS dates on shell beads from Grotta del Cavallo yielded 45,010–43,380 cal BP for the lower Uluzzian layer. If the dates and the taxonomic attribution are accepted, they would extend the period of Neandertal-modern human coexistence to some millennia. Neandertals are thought to have persisted in southern Iberia until 37 ka, based on the dates for Middle Paleolithic assemblages there [66] and at other sites in Europe based on dates for Neandertal remains at Spy (Belgium) and Vindija (Croatia). Elsewhere the dates for the Campanian Ignimbrite ash horizon, stratigraphically above several Proto-Aurignacian layers, situate the end of the Middle Paleolithic at about 40 ka (see *The date of the demise*).

The “transitional” industries are extremely relevant to understand the routes of migrations and expansion of AMH in Europe, the nature of cultural contacts between the local and immigrant populations and the onset of the Upper Paleolithic in those regions. However, we need more contextual (i.e. stratigraphic, technological and in some cases fossil) data before we can make accurate assessments of the evidence, e.g. in terms of the type of hominin authorship [62]. In the case of the Châtelperronian, attributed to Neandertals by several scholars, we will review recent evidence from sites where stratigraphic admixture can be excluded and are less controversial than Grotte du Renne.

Results

Explanations for the demise of Neandertals have been developed at various levels of abstraction, and include topics notoriously difficult to study in the archaeological record, such as “complex symbolic communication systems” [28], “fully syntactic language” [67] or “cognitive capacities” in general. Other hypotheses refer to behavioral domains which do leave clear traces in the archaeological record, provided the right taphonomic conditions prevail (Table 1; Text S1, Hypotheses 1–11).

Language and Symbolism

The archaeological record has been mined in various ways to produce evidence for symbolic aspects of human culture, with a strong focus on the emergence of language. Archaeological finds from the MSA have been used to build scenarios for the timing and location of the origin(s) of language. Several of these finds come from South Africa and include engraved pieces of ochre from Blombos Cave [68]–[69], *Nassarius* shells from the same location [70], and heated silcrete artefacts from the site of Pinnacle Point, said to testify to sophisticated pyrotechnological know-how by early modern humans [36]. Botha has shown the assumptions and series of inferential steps some of these authors had to make before being able to squeeze “language” out of their mute artefacts [71]–[72], see also [73]–[74] pinpointing the weak spots in the steps leading from observations about archaeological phenomena to statements about the presence of “fully syntactical language”. Moreover, recent data on Neandertal use of ochre and manganese as well as on Neandertal production of pitch, the presence of transported and ochre-smeared shells, of ornaments such as eagle claws and perhaps bird feathers [75]–[78] (Text S1, Hypothesis 1), and the production of the specialized bone tools recently reported from two late Middle Paleolithic sites [79] (Text S3, Lissours) indicate no significant differences between the MSA data commonly used to create these more abstract explanations and the later Middle Paleolithic record.

The same applies to explanations regarding behavioral domains which do leave clear traces in the archaeological record. In our study none of the explanations listed in the introduction and in Table 1 proved to be supported by adequate archaeological data.

Hunting Methods and Diet

With the demise of the idea that Neandertals were scavengers and ineffective hunters [80]–[82], the former interpretive framework has to some degree been reformulated in terms of Neandertals inferiority in subsistence strategies and hunting weaponry for which, again, there is no support from the archaeological record (Text S1, Hypotheses 3–4). Neandertals were by all means accomplished large game hunters, who survived in a wide range of environments subsisting by hunting a wide range of animals in a variety of topographical settings. In contrast to prevailing ideas [31], [83], their diet was not restricted to large and medium size herbivores only. Several sites document a broader diet, including aquatic foods, small fast game (birds, rabbits) as well as plant resources (*SI Hypothesis 5*). Likewise, the idea that spear throwers and bow and arrow were first developed in the MSA of South Africa before 60 ka and conferred substantive advantages on modern humans as they left Africa and encountered Neandertals equipped with only hand-cast spears [33], [84] may be correct, but there is no solid archaeological evidence in its support (Text S1, Hypothesis 4.3).

Organized Use of Space

The same applies to purported differences in the use of space at the level of camp sites by AMH and Neandertals, with organized use of space seen as typical for AMH. The South African MSA record has some cases of excellent preservation of plant materials in dry conditions, including possible bedding material recovered from 77 to 58 ka old deposits at Sibudu [85]–[86]. Some researchers have taken the presence of bedding material and “the deliberate use and organization of living space” to be “an important trait of culturally modern behavior” [87]. However, there exists good evidence for well-delimited activity areas at Neandertal sites such as Kebara, Amud (Israel) and Tor Faraj (Jordan) as well as from several European sites where the task-specific areas are documented by refitting (Text S1, Hypothesis 3). Furthermore, bed building by great apes is a well-documented learned behavior, dependent on appropriate early experiences [88].

Capacity for Innovation

Another prominent scenario suggests that the archaeological record of sub-Saharan modern humans, to wit of the two main technocomplexes of the South African late MSA, the Still Bay (SB) and the Howiesons Poort (HP), indicates very dynamic and innovative phases which lasted less than 10,000 years each [26], [89]. These would constitute a striking contrast to the record of the Neandertals, who supposedly lacked the capacities to innovate and “made the same kinds of tools for 200,000 years without ever tinkering with the basic components” [90]. Recently reported dates from the Diepkloof site (South Africa) are significantly complicating our views on cultural change in the Late Pleistocene there, however. According to these new dates [91]–[92] the SB and HP technocomplexes would have a much longer duration than previously envisaged [89], comparable to those of broadly contemporaneous Middle Paleolithic industries in Europe, which show clear spatio-temporal distributions (Table 2, Text S1 Hypothesis 2). Jacobs’ OSL age estimates for the SB and HP are considered controversial by some [93]. More dating work is clearly required, while systematic technological and typological analyses are necessary to dispel doubts about assemblage definition, especially for the MIS 5 occurrences.

Technological phases	Start (ka)	End (ka)
Still Bay		
Romman	ca 75.5 (OSL)	67.8 (OSL)
Stubb	70.3 ± 2.9 (OSL)	
Diepkloof	106 ± 19 (TL)	
Howiesons Poort		
Stubb	64.7 ± 2.5 (OSL)	61.7 ± 2.2 (OSL)
Klein River Main Site, Cave 1A	64.3 ± 3.8 (OSL)	56 ± 3 (TL)
Binder Cave	76 ± 4 (OSL)	60 ± 3 (OSL)
Diepkloof	105 ± 19 (TL)	55.5 ± 3 (TL)
Post-Howiesons Poort/MSA III (2)		
Klein, Cave 1A	60 ± 3 (TL)	—
Klein, Cave 1A	57.9 ± 5.3 (OSL)	—
Binder Cave	60 ± 3 (OSL)	44–42 (1 ^σ C uA BP)
Stubb	58.3 ± 1.4 (OSL)	58.8 ± 1.9 (OSL)
Broomfield	ca 56 ± 6 (2 ^σ series)	58–56 (1 ^σ C uA BP)
Klein Kliphuis	57.8 ± 3.4 (OSL)	53.3 ± 1.3 (OSL)
Rose Cottage	56.0 ± 3.3 (OSL)	—
Neolithic in Western Europe (1)		
Neolithic of Achéulian Tradition 100 sites in SW France	70	40
Quina Mousterien 100 sites in SW France	70	40
The Acheulean/Neolithic (11 sites in Germany, Poland and the Czech Republic)	80	50

(1) After [89,91–92,94,95–100]. We have excluded assemblages with uncertain stratigraphy (Simonsburg, HP layers at Klein Kliphuis) or unpublished dates (Yellow Rock Shelter).

(2) The term Post-Howiesons Poort is equivalent to MSA III at Klein River Main Site. It includes informal designations of the Stubb sequence (such as late MSA and final MSA) and have not included several TL and OSL dates for the HP and Post-HP of Rose Cottage because they are inconsistent or only informative for the middle part of the sequence (710–100). The Post-HP OSL date reported here for Rose Cottage (80) is of layer LPI which is toward the base of the Post-HP sequence but above its oldest layer.

(3) The Middle Paleolithic technocomplexes are dated by TL, OSL, ¹⁴C calibrated BP and chronomagnetism.

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Table 2. Dates of technological phases in the late Middle Paleolithic of Europe and in the late Middle Stone Age of South Africa (a).

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In contrast it is clear that the Post-HP technocomplex, characterized by unifacial points on flakes (Sibudu) or blades (Border Cave, Klasies), hard hammer percussion, rare presence of the Levallois technique and of formal tools on blades (Klasies) and flakes (esp. Rose Cottage and Sibudu), has a duration of about 20,000 years; even more if “transitional” or late MSA sites in South Africa, dated between 40 and 20 ka, are taken into account. These include three layers at Rose Cottage, dated between ca 30.8 and 27 ka, and Strathalan Cave B, with two layers dated between 29 and 25.7 ka [94]. OSL and ESR dates for post-HP assemblages are supported by AMS radiocarbon dates. Thus the pace of change and the evolutionary patterns of the European Upper Pleistocene record, which shows regional differentiation, cultural traditions and technological changes through time, are comparable to what is known from the African record. Technological and tool-type changes in the Mousterian industries precede by far the advent of Proto-Aurignacian and Aurignacian industries. Whatever dates are accepted for these industries [95], changes in Mousterian industries occurred long before 50 ka.

Size of Social Networks

Other workers have suggested that Neandertals and AMH differed significantly in the sizes of their social networks. AMH larger-scale social networks are supposed to have acted as a buffer against environmental downturns, thus fostering long term survival. Such inferences are based on the translation of distances over which artifacts were transported in the deep past into statements about former mobility strategies, exchange systems and sizes of social networks. Yet it is almost impossible to differentiate between long distance transport as a signature of direct procurement as opposed to indirect acquisition, such as through trade or exchange networks [107]. Our review of the evidence (Text S1, Hypothesis 7) shows that as far as the archaeological record for raw material transfer distances is concerned, the MSA and the Middle Paleolithic record are not significantly different, despite of the obvious ecological differences between western Eurasia and Africa.

Hafting Procedures, Heat Treatment and Cognition

According to another hypothesis Neandertals hafting of tools was a simple procedure, only using naturally available glues. Early modern human hafting techniques entailed complex procedures which required “abstract reasoning” and are hence indicative of modern cognition. According to Wynn and Coolidge [41] evidence for complex hafting procedures dates back to about 70 ka in South Africa. Replication experiments suggest that HP hunters used a mixture of plant gum, beeswax and powdered ochre to produce an adhesive that had to be carefully dried using fire [37]. However, from 200,000 years ago onward, European Neandertals used fire to synthesize pitch from bark, through a process that involved distillation in the absence of oxygen and within a temperature interval of 340°C–400°C [108]. Pitch is not a naturally occurring glue; it is a man-made material produced using fire as a tool. Birch bark pitches have been experimentally produced in small dug out and subsequently covered pits beneath camp fires [109], though in very small quantities only, leaving open the question how exactly Neandertals produced their pitches. Two flakes associated with elephant remains at the Italian site of Campitello (Tuscany, Italy) were found enclosed in blackish organic material that was analyzed by gas chromatography/mass spectrometry and identified as a pitch obtained by a pyrolysis-type process of birch bark for hafting the flint flakes [110]–[111]. The Campitello finds date to the end of MIS 7. Comparable finds of birch bark pitch come from the German site Königsau A, with an estimated age of 80 ka [112]–[113]. On basis of the stratigraphy of the site, the AMS dates of 43,800±2100 BP and 48,400±3700 BP cited in ref [113] should be considered minimum ages.

Mania's fieldwork at the site produced two pieces of pitch, one with fingerprints as well as the imprint of a stone tool and a wooden haft. Experimental studies show that production of pitch in the absence of air-tight pottery containers requires a high degree of technical knowledge.

According to Brown et al [\[36\]](#) heat treatment of silcrete at the South African site of Pinnacle Point at c. 72 ka and possibly as early as 164 ka indicates sophisticated knowledge of fire and elevated cognitive abilities that may have been a behavioral advantage on Neandertals as early modern humans moved to Eurasia. The evidence of pitch production as early as 200 ka by European Neandertals shows that those "elevated cognitive abilities" were not the exclusive domain of modern humans.

The straightforward scenario of superior AMH moving into Neandertal territory is also complicated by the Late Pleistocene occupation history of the East Mediterranean Levant. AMH were present in that region between 80 and 130 ka, and created the Skuhl and Qafzeh record with its burials, pigments and personal ornaments [\[114\]](#), associated with a Middle Paleolithic lithic technology. Between 80 and 47 ka however, only Neandertals are known from the fossil record of the Levant [\[115\]](#). If the absence of fossil AMH in the record represents a true absence from the region, this could indicate that the Skuhl/Qafzeh hominins and their immediate descendants indeed may have "lacked the behavioral capacities that enabled subsequent modern humans to compete successfully against the Neanderthals" [\[115\]](#).

Discussion

We conclude that all the "archaeology-based" explanations for the demise of the Neandertals reviewed here ([Table 1](#), [Text S1](#), Hypotheses 1–11) are flawed. They were based on much less data than we have available today and were at least in part the result of a long tradition of thinking in terms of Neandertals-AMH dichotomies, steered by overstressing developments within the Upper Paleolithic of Europe, the record of which has become almost like a yardstick for modern human behavior ([Text S2](#)).

While the debate about AMH dispersal times and routes out of Africa is intense, based on a range of archaeological as well as genetic data, the archaeological record from the various continents does not provide strong support for any of the suggested routes nor any of the suggested factors in the demise of the Neandertals. The very fact that the migration time estimates vary so widely suggests that we simply have no solid data; perhaps there was more than one migration event (in addition to the Last Interglacial limited expansion in the Levant), and in all probability the migrating groups did not have a strong cultural homogeneity. This may explain why we do not see clear archaeological signatures for AMH on the move.

Interestingly, the widely accepted date of 60 or 50 ka for the modern human expansion into Eurasia (following the earlier short-lived exodus in the Levant documented at Skuhl and Qafzeh) would rule out South Africa as the location for source populations for two reasons: (i) by 60 ka the HP tradition of backed tools made on blades and bladelets produced by soft stone hammer (supposedly associated with the AMH expansion) had given way to the post-HP assemblages characterized by a variety of flake tools and blades produced by hard hammer percussion but without backed blades [\[94\]](#), [\[103\]](#), [\[105\]](#), [\[116\]](#); (ii) the Still Bay and HP populations were not larger than other MSA populations and might even have been

smaller, thus excluding population pressure as the prime mover of the migration [117]. According to Klein [11] the Out of Africa expansion was underlain by a neural mutation that promoted the final development of the modern human brain. Direct evidence for this hypothesis may come from comparisons of Neandertal and modern human genomes.

In the recent past, much debate has been generated from the observation that Neandertals began to produce a richer archaeological record, including bone tools, personal ornaments and use of manganese and ochre, at the time when AMH started colonizing Europe. Some interpreted this change in the record as the result of Neandertal absorption of ideas and techniques from the incoming AMH. After having produced a rather monotonous record for almost 300,000 years, an independent invention of these new items just at the time of the arrival of AMH would have to be seen as an “impossible coincidence” [28]. However, as reviewed here, use of ochre, of personal ornaments, production of specialized bone tools and complex hafting techniques were part of the Neandertal repertoire already before the arrival of AMH in western Eurasia.

The present review also suggests that some of the innovative technologies of the Protoaurignacian and of the Aurignacian may have developed out of a Middle Paleolithic base (for a similar viewpoint, see [118]). Some components that occur sporadically or episodically in Neandertal and late MSA assemblages become much more common later, like pigment use, symbolic objects, extensive transport of raw materials and even specialized bone tools [79]. The same goes for another element, the intentional production of bladelets (<4 cm in length) from bladelet cores. Bladelets have been considered a discriminant factor between the Upper and Middle Paleolithic and therefore between AMH and Neandertals [119]. Production of bladelets has been securely identified in French Mousterian assemblages, e.g. at Combe Grenal (layers 30–29 and layers 16 and 14), Champ Grand and Grotte Mandrin, and in Spain at sites such as El Castillo and Cueva Morin [120], [121]. All these assemblages belong to the final Mousterian, with the exception of Combe Grenal and Grotte Mandrin; at the latter site, a layer with blades, bladelets and microlithic points is overlain by five layers with flake-based Mousterian assemblages [121]. At Combe Grenal layers 29–30 have an estimated age of late MIS 4, i.e. around 60 ka. Bladelets and bladelet cores are not abundant (5% of the assemblage at Combe Grenal layers 29–30), yet they show that Neandertals, like late MSA humans and the makers of the Protoaurignacian, mastered the technology of bladelet production, albeit using methods different from the HP small blade technology. It is their frequency, not cognition or technical competence, that distinguishes AMH bladelet production from that of Neandertals [120]. The techniques and methods of bladelet making in the Mousterian are different from those of the Protoaurignacian, just as the kind of possible symbolic objects are also different (use of raptor claws; on perforated or grooved animal teeth (see Text SI, Hypothesis 1). Perhaps the nature of the contacts should be seen in terms of diffusion of ideas rather than as face to face interaction and the copying of specific objects [122]. The occurrence of Dufour bladelets (often used as projectile elements in the Aurignacian and the Protoaurignacian) with very specific techniques of manufacture in the Châtelperronian of Quincay is interpreted in a similar way, as a form of low-degree social interaction between Neandertals and modern humans [123].

The Date of the Demise

Various new dates support the idea of some chronological overlap between AMH and Neandertals, which may have enabled interbreeding and cultural interaction in western Europe: AMS dates on ultrafiltered bone collagen from the Châtelperronian layers X and IX

of Grotte du Renne at Arcy, c. 44 to 41 kyr cal BP; the date of the Saint-Césaire Neandertal at 41.9–40.6 kyr cal BP [63]; the fact that the Protoaurignacian at the Italian sites of Castelcivita and Serino is overlain by the Campanian Ignimbrite tephra, dated to 39.28 ± 0.11 ka by $^{40}\text{Ar}/^{39}\text{Ar}$ [124]; the modeled age ranges of c. 41.5–39.9 kyr cal BP of several radiocarbon-dated Proto-Aurignacian sites [95]; the date of the Oase 2 early modern cranium at c. 40 ka [125]; the AMS dates for the Neandertal child from Spy cave (Belgium), 36,870 to 38,494 and 37,297 to 40,490 cal BP [126]; the AMS dates for the Vindija (Croatia) Neandertal remains at c. 38 kyr cal BP [127], [128]; the 37.4 ka cal BP date for the final Mousterian level of Cueva Antón in southeastern Spain [75]. Even if we do not consider dates judged by some as controversial such as (i) the AMS dates on shell beads for the layer containing the modern human teeth at Grotta del Cavallo at 45,010–43,380 cal BP [5, contra 2]; (ii) the dates for the Kent's Cavern modern human maxilla [3, contra 2, 129]; and (iii) the dates for the Aurignacian at Geissenklösterle at c. 42 kyr cal BP [4, contra 2], some millennia of overlap are indicated. The latest Neandertal currently known from the Levant is the adult male skeleton from Amud Cave (Israel) with an ESR date of 53 ± 8 ka on tooth enamel [130].

Interbreeding and Assimilation

For some authors replacement and supposedly rapid extinction of Neandertals can be explained only in terms of substantial cognitive, technological and demographic differences between the Neandertals and AMH [42], [131]. But, as we tried to show here, the Neandertal archaeological record was not different enough to explain their demise in terms of inferiority in archaeologically visible domains. Thus, if Neandertals were not technologically and cognitively “disadvantaged”, how can we explain that they did not survive?

Some modern human-like anatomical characteristics are said to occur in late Neandertal fossils (as in the Vindija, St. Césaire and Riparo Mezzena late Neandertals [132], [133] and refs therein) and vice versa some Neandertal features are present in early specimens of modern humans in Europe [134], [135] supporting a hypothesis of some degree of admixture between the two groups. However, until recently the morphological evidence of admixture was often dismissed. In 2010 a draft sequence of the Neandertal nuclear DNA provided clear evidence of interbreeding between Neandertals and modern humans [48], estimating that Neandertal inheritance makes up 1–4% of the genomes of people outside of Africa. A revised estimate based on a high-coverage sequence of a Neandertal from the Altai Mountains now suggests 1.5–2.1% [49]. Genes of Neandertals may have been favored through natural selection, and possibly played a role in the development of the immune system of modern humans [136] or in UV-light adaptations [137]. According to [138] gene flow from Neandertals to modern humans occurred between 47,000 and 65,000 years ago, and most likely happened at the time when Neandertals and modern humans encountered each other in Europe and the Middle East around 50,000 years ago.

In sum, interbreeding and assimilation, the tenants of a model first proposed by Fred Smith [139] are now supported by genetic data [134], [140]. It can be argued that the level of interbreeding may have been too limited to support an assimilation scenario. An interestingly parallel to this complex situation can be found in another “revolution”, the so-called Neolithic Revolution [43], [141], which does not feature explanations in terms of “cognitive” differences. The first farmers swept into Europe from the Near East at about 7500y BP displacing the local Late Mesolithic hunter-gatherers. But the Mesolithic hunter-gatherers, who cannot be described as cognitively inferior, were not submerged by hordes of farmers. Farmers and foragers coexisted for thousands of years in NW Europe; in Central Europe local

hunter-gatherers adopted farming but in southern Scandinavia local foragers retained the Mesolithic lifestyle for c. 1500 years after farming arrived in Central Europe [142], [143]. Cultural contact is suggested by clear continuities in flint technology between the Mesolithic and early Neolithic in the region. After a very complex pattern of expansions and genetic shifts of the last 8,000 years the hunter-gatherer mitochondrial DNA haplogroups form 16% of the present-day Central European genetic composition [143]. It would take at least one millennium between the first arrival of immigrants and a notable increase in their population size.

The original Neandertal contribution to modern human biology may have been larger 40,000 years ago - equivalent to 2000 generations (with generation time at 20 years) – than estimates based on genomic regions of present-day humans suggest [144], [145]. Interbreeding of Neandertals and modern humans may have helped modern humans to adapt to non-African environments but also introduced alleles that were not tolerated and contributed to male hybrid sterility thus reducing the proportion of Neandertal ancestry of the period of contact to that seen today [144].

Mitochondrial genetic diversity of eight early modern European humans dated to ca 38,000 to 4,500 (¹⁴C cal BP, from Kostienki 14 to Ötzi The Iceman) is 1.5 times higher than that of five European Neandertals spanning the time to 38 to 70 ka [23], [146]. The high coverage genome of the Altai Neandertal [49] also suggests low genetic diversity which could indicate small population sizes (see [Text S1](#) Hypothesis 8 for archaeological data). These genetic data suggest that differences in population sizes between the “resident” Neandertals and incoming AMH populations may have been a contributing factor in the absorption of Neandertal populations [23]. The momentous cultural changes that followed the arrival of AMH in Western Eurasia were not uniquely due to the residents’ cognitive or technological inferiority causing rapid and total replacement. The Neandertal demise appears to have resulted from a complex and protracted process [147] including multiple dynamic factors such as low population density, interbreeding with some cultural contact, possible male hybrid sterility and contraction in geographic distribution [148] followed by genetic swamping and assimilation by the increasing numbers of modern immigrants.

Conclusion

In a review of the MSA and Middle Paleolithic archaeological record we have shown that inferred markers of modern human cognitive and behavioral capacities have a greater time depth in the Middle Palaeolithic record than commonly acknowledged. We have found no data in support of the supposed technological, social and cognitive inferiority of Neandertals compared to their AMH contemporaries. The results of our study imply that single-factor explanations for the disappearance of the Neandertals are not warranted any more, and that their demise was clearly more complex than many archaeology-based scenarios of “cognitive inferiority” reviewed here seem to suggest. This has implications beyond the field of archaeology per se: archaeologists’ characterizations of Neandertals as cognitively inferior to modern humans [149] have created an interpretive framework within which subtle biological differences between Neandertals and modern humans tend to be overinterpreted (see for instance [150]).

After 40,000 years and 2000 generations the Neandertal fraction in non-African modern human genomes still constitutes a substantial legacy from these ancient hominins who differed from contemporary AMHs in both geno- and phenotypes [151] but whose

archeological record was not different enough to support the purported cognitive “gap” between them and their contemporary modern humans.

Source: <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0096424>

Homo erectus, our ancient ancestor

By Lisa Hendry

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The extinct ancient human *Homo erectus* is a species of firsts. It was the first of our relatives to have human-like body proportions, with shorter arms and longer legs relative to its torso. It was also the first known hominin to migrate out of Africa, and possibly the first to cook food.

In terms of species survival, *Homo erectus* is a huge success story. Fossil evidence for *H. erectus* stretches over more than 1.5 million years, making it by far the longest surviving of all our human relatives.

Compare this to our own species, *Homo sapiens*, which has been around for perhaps 400,000 years so far, and we begin to appreciate their ability to survive over a long period marked by many changes to the environment and climate.

H. erectus was also the most geographically widespread species apart from *H. sapiens*. *H. erectus* appeared in Africa about two million years ago, evolving from either a late form of australopith or one of the more primitive forms of *Homo*, and went on to spread into many parts of Asia.

Scientists disagree over how *H. erectus* and *H. sapiens* relate to each other, but most agree that *H. erectus* can be called an ancestor of modern humans.

Homo erectus facts

- **Lived:** from about two million years ago until at least 250,000 years ago
- **Where:** Africa, Asia and perhaps Europe
- **Appearance:** human-like body proportions and upright stance, a protruding brow ridge, large face and no chin
- **Brain size:** about 550-1,250cm³
- **Height:** about 1.4-1.8m
- **Weight:** about 41-65kg
- **Diet:** meat (initially from scavenging but later potentially also from hunting) and plants
- **Species named in:** 1893 (as *Anthropopithecus erectus*, renamed *Pithecanthropus erectus* in 1894 and *Homo erectus* in 1950) following its 1891 discovery
- **Name meaning:** 'upright human'

When did *Homo erectus* live?

H. erectus is the longest lived of all human species. Although some researchers believe that what we now know as *erectus* consists of several distinct species (including *Homo georgicus* and *Homo ergaster*), most accept a broad diagnosis of the species.

The earliest fossils that are complete enough to display the anatomical pattern of *H. erectus* are from eastern Africa and western Asia, and are about 1.5 to 1.9 million years old. The conventional view is that the species evolved in Africa about two million years ago.

Precisely when - and why - *H. erectus* disappeared is unclear, but it appears to have survived in parts of Indonesia until at least 250,000 years ago.

Disputed evidence of the very late survival of *H. erectus* on the Indonesian island of Java exists in the form of fossil braincases (the part of the skull that encloses the brain) and a few other fragments. Some methods have dated these to older than 200,000 years, others to less than 50,000 years. The fossils show the characteristic *H. erectus* anatomy, but display brain sizes up to 50% larger than earlier examples of the species from the island.

Where did *Homo erectus* live?

Current evidence suggests all hominins before *H. erectus* lived in Africa. However, almost as soon as this species appears in the fossil record there is evidence it expanded out of Africa and into western Asia, then to eastern Asia and Indonesia.

A small skull fragment from East Turkana, Kenya, dates to about 1.9 million years ago, supporting an African origin. But the first fossils were found in Asia, and it is in Asia where this species survived for so long.

Fossil evidence for *H. erectus* in western Asia comes from exciting finds, made at Dmanisi in Georgia from 1991 onwards, that are about 1.8-1.85 million years old.



Cast of skull 5 (D4500) - the most complete *Homo erectus* skull found at Dmanisi, Georgia - on display in the Museum's [Human Evolution gallery](#). The original fossil skull is about 1.8 million years old.

The species spread into eastern Asia, including China, where it appears to have been present until at least 300,000 years ago.

In southeast Asia, *H. erectus* was a long-term inhabitant of Java. *H. erectus* fossils there date from about 1.6 million years to at least 250,000 years ago.

The species may have survived more recently in Taiwan, the Philippines and on the Indonesian island of Sulawesi, but the evidence isn't conclusive.

We don't know whether *H. erectus* reached Europe. But since the assortment of animal fossils found at Dmanisi closely resembles the forest and grassland fauna of southern Europe from the same time, an early human settlement of that region is at least a possibility.

Why did *Homo erectus* leave Africa?

Dispersal of species happens for many reasons but essentially *H. erectus* probably drifted across northern Africa, across the Sinai Peninsula into Asia, when environmental changes meant suitable habitats and food sources stretched that far.

For example, sabre-toothed cat remains were found alongside *H. erectus* fossils in Georgia. The cats apparently dispersed from Africa. These specialised carnivores lacked the teeth to strip a carcass clean of its meat, so might have provided scavenging opportunities for early humans following them out of Africa.

It is likely that the spread of *H. erectus* as far as Java, across what are now islands of Southeast Asia, was possible because these were connected at the time.



Java was intermittently connected to the Southeast Asian mainland, allowing *Homo erectus* to take up residence there. The species survived on Java for a very long time, until at least 250,000 years ago. © Mohd Farid/Shutterstock.com

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Meat was an important part of the diet of *H. erectus* and some carnivorous animals range more widely than herbivores. This, together with their larger body size, may explain the broad geographic range of *H. erectus*.

***Homo erectus* characteristics**

The species *H. erectus* is highly varied - not surprising considering it existed for so long and over such a wide area.

H. erectus is the oldest known species to have a human-like body, with relatively elongated legs and shorter arms in comparison to its torso. It had an upright posture.

By studying the remains of the very complete skeleton known as [Turkana Boy](#), scientists have concluded that *H. erectus* walked and ran in much the same way as we do.



Replica of the skeleton known as Turkana Boy and Nariokotome Boy on display at the Field Museum of Natural History, Chicago, USA. It is the most complete early *Homo* specimen ever discovered. © James St John, licensed under [CC BY 2.0](#) via [Flickr](#).

[Read more](#)

Individuals were comparable to humans today in terms of body size and shape, although they were more muscular and had much wider hips. Adults grew to about 1.4-1.8 metres tall and weighed 41-65 kilograms.

H. erectus brain size was smaller than that of humans today - in some cases nearly half the size - and their skulls were thicker.



From left to right: skulls of *Homo erectus*, *Homo heidelbergensis*, *Homo neanderthalensis* and *Homo sapiens*. The braincase of *H. erectus* was more elongated than that of later humans. It had a prominent brow ridge, like *H. heidelbergensis*.

[Read more](#)

Early *H. erectus* had smaller, more primitive teeth, a smaller overall size and thinner, less robust skulls compared to later specimens.

The species also had a large face compared to modern humans. Like Neanderthals, their skull was long and low, rather than rounded like our own, and their lower jaw lacked a chin.

A prominent brow ridge was present over the eye sockets. Virtually all archaic humans have a brow ridge - this feature reached its maximum size in some *H. erectus*.



Cast of *Homo erectus* skullcap (top part of a skull) from China showing the prominent brow ridge of this species, on display in the Museum's Human Evolution gallery

What were brow ridges for?

There has been a lot of debate about what function the brow ridge had, if any.

Most ideas concentrate on its role as a feature that strengthened the skull or helped dissipate forces passing through the skull. Researchers have recently indicated the latter was unlikely, instead speculating that it may have had a role in social signalling between archaic human individuals, enhancing friendly or aggressive facial expressions.

What tools did *Homo erectus* use?

H. erectus was the first human species to make handaxes (Acheulean tools). These were sophisticated stone tools crafted on two sides. They were probably used to butcher meat, among other purposes.

Prior to that, the tools of ancient humans and their predecessors, including those of the first known *H. erectus* (at Dmanisi, for example), were much more primitive - simply rock flakes knapped to a sharp edge.



Foreground: Acheulean tools first made by *Homo erectus*, on display in the Museum's Human Evolution gallery. These two-sided handaxes were complex stone tools that continued to be made for more than a million years. Background: more primitive tools.

[Read more](#)

What did *Homo erectus* eat?

Early *H. erectus* was equipped with a simple set of stone tools that looks best suited to scavenging meat. Later *H. erectus* peoples produced a wider range of stone tools and were probably active hunters.

Some experts believe that the long-legged physique of *H. erectus* evolved to facilitate long-distance jogging and running across open country to acquire meat.

While meat formed a key part of their diet, it is likely that plant resources were also important and they lived as hunter-gatherers.

Did *Homo erectus* use fire?

The use of fire is an important milestone in human evolution, granting access to light, warmth, protection from predators and the ability to cook food - each of which aids survival.

Scientists don't know when humans were first able to make fire at will. Early humans probably captured natural fires and kept them alight for as long as they could.

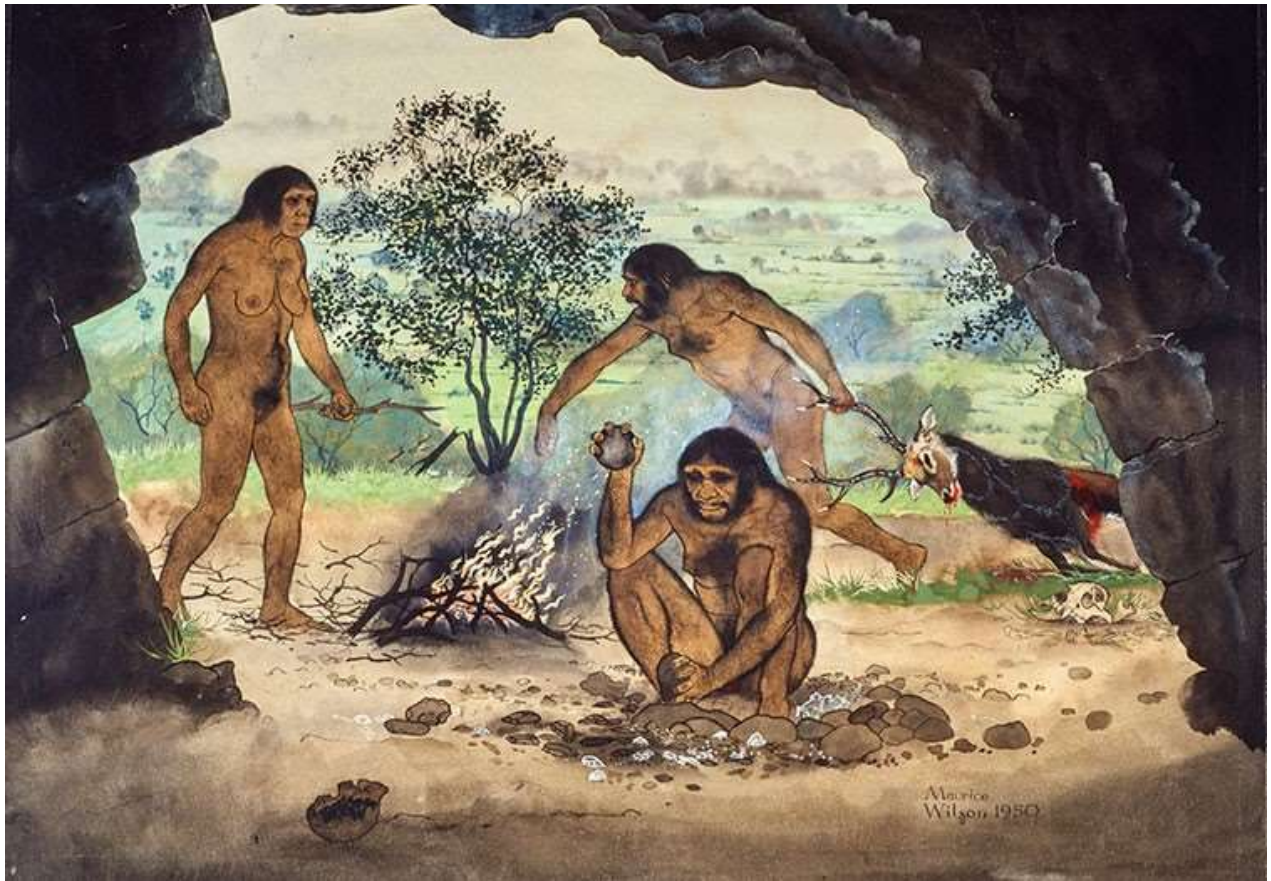


Illustration by Maurice Wilson showing *Homo erectus* using fire and preparing tools

H. erectus may have been the earliest human relative to have controlled fire.

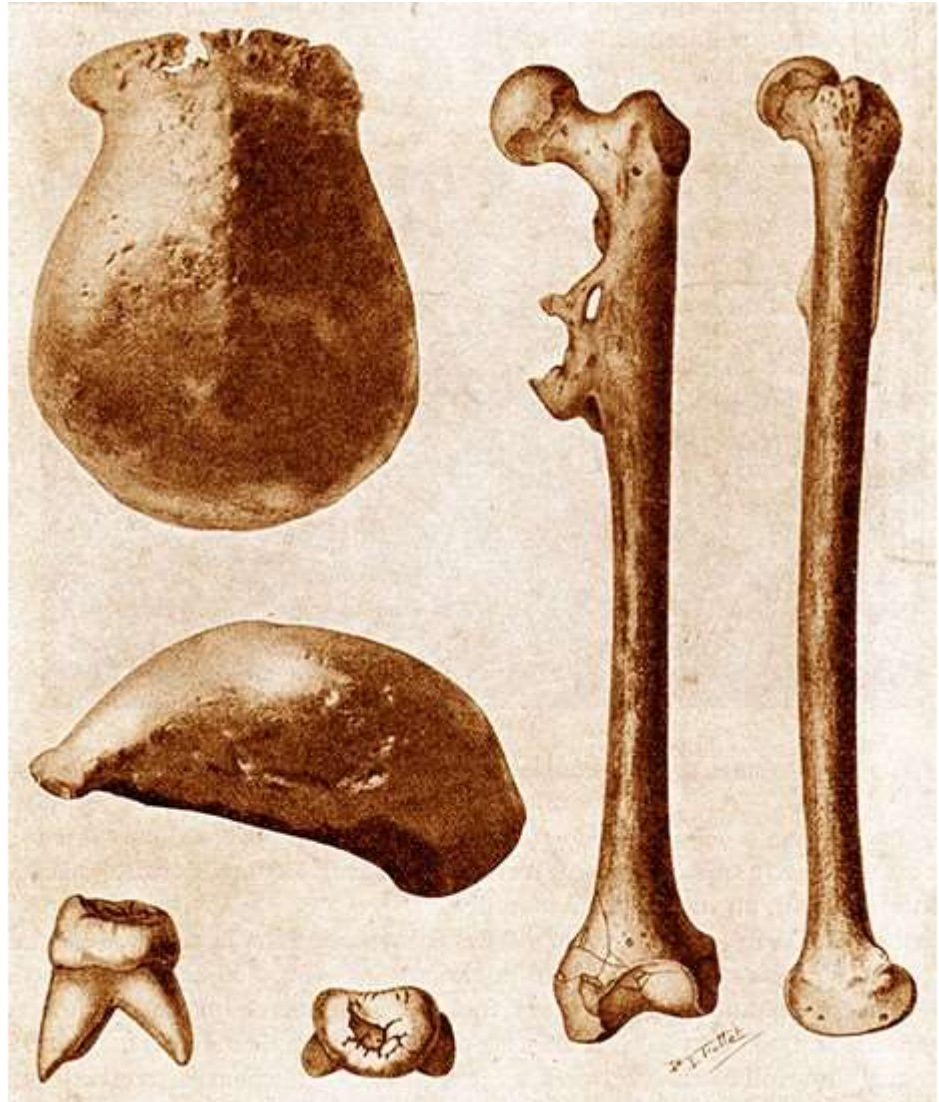
Evidence is quite thin on the ground, but for example, researchers found [evidence of ash as well as burnt bone fragments](#) in a one-million-year-old sediment layer in the Wonderwerk Cave in South Africa. The site is too far inside a cave for the ash to be caused by a lightning strike and the spontaneous combustion of bat guano was ruled out.

History of *Homo erectus* discovery

The first *H. erectus* fossils were found in 1891 on the Indonesian island of Java by a Dutch doctor called Eugène Dubois.

Before these discoveries, Neanderthals were the only early human for which fossils had been found.

Dubois unearthed an isolated tooth (Trinil 1) and - most importantly - the top part of a skull (Trinil 2) and a thigh bone (Trinil 3). Together they have often been referred to as Java Man.



Drawing of the first *Homo erectus* fossils found in 1891 on Java, showing the tooth (Trinil 1), skullcap (Trinil 2) and thigh bone (Trinil 3), from [Wikimedia Commons](#)

The thigh bone indicated the creature had an erect, human-like posture, but the skullcap indicated its brain was much smaller than humans today and featured a distinct brow ridge.

By 1940 many more *H. erectus* remains had been unearthed, both in Java and China.

Dmanisi discoveries and *Homo georgicus*

From 1991, surprising new finds were being made at Dmanisi in Georgia. Under the remains of a medieval village, archaeologists found a variety of extinct fauna, including ostriches, primitive deer, rhinoceroses, large carnivores and a human lower jaw.



Dmanisi castle, with Sioni Cathedral and archaeological site - where important *Homo erectus* finds have been made - in the background © Larry V Dumlao, licensed under [CC BY-SA 4.0](#) via [Wikimedia Commons](#)

[Read more](#)

Further excavations and research indicate the material is about 1.8-1.85 million years old. The site has now produced five small-brained human skulls, three more jawbones and many other parts of the skeleton, as well as simple stone tools.

The skull shape looks like a primitive version of the *H. erectus* morphology, while the leg bones are relatively small, indicating an adult body size of only about 1.5 metres and a weight of about 45 kilograms.

Some researchers believe that the distinctive features of the Dmanisi fossils (including the smaller body and brain sizes) point to this being a more primitive species than *H. erectus*, which could be called *Homo georgicus*. However, others feel that these features simply reflect its position as a very early member of the species *H. erectus*.

Important *Homo erectus* fossils

Although Java Man was the first *H. erectus* discovery, the find that has revealed most about this species is Turkana Boy.

- **Turkana Boy (KNM_WT 15000 skeleton)**
The skeleton of a young *H. erectus* male discovered at Nariokotome in the West Turkana region of Kenya. Unearthed in 1984, the skeleton is around 1.5 million years old and represents the most complete ancient human specimen ever discovered. Investigations

show that although the boy was only about nine years old, he was nearly fully grown. He was 1.6 metres tall when he died.

- **Peking Man fossils**

A set of around 200 *Homo erectus* fossils from more than 40 individuals unearthed at the Zhoukoudian archaeological site near Beijing in the 1920s and 1930s. They were originally assigned to the now-obsolete group *Sinanthropus pekinensis*. The fossils, which included several relatively complete skulls, went missing during the Second World War. Fortunately, casts had been made. The site has been dated to 780,000 to 400,000 years ago.



Reconstruction of one of the Peking Man *Homo erectus* fossils excavated from China. Most of the original fossils were lost in World War Two.

- **Dmanisi skulls**

Five *H. erectus* skulls were discovered at Dmanisi in Georgia from 1991 onwards. They look quite different from each other, but analysis by researchers shows that the amount of variation is comparable to that seen among modern people or chimpanzees.



Dmanisi fossils D2700 (skull 3) and D2735, around 1.8 million years old. The Dmanisi skulls look like an early form of *Homo erectus*. © Gerbil, licensed under [CC BY 3.0](#), via [Wikimedia Commons](#)

This article includes information from Our Human Story by Dr Louise Humphrey and Prof Chris Stringer.

Source: <https://www.nhm.ac.uk/discover/homo-erectus-our-ancient-ancestor.html>

Of course, the Homo erectus has the same problems: Not enough time between it, and the modern human, to evolve.

Skull of Homo erectus throws story of human evolution into disarray

This article is more than 9 years old

A haul of fossils found in Georgia suggests that half a dozen species of early human ancestor were actually all Homo erectus

[Ian Sample](#), science correspondent
[@iansample](#)

Thu 17 Oct 2013 19.00 BST

The spectacular fossilised skull of an ancient human ancestor that died nearly two million years ago has forced scientists to rethink the story of early human evolution.

Anthropologists unearthed the skull at a site in Dmanisi, a small town in southern Georgia, where [other remains of human ancestors](#), simple stone tools and long-extinct animals have been dated to 1.8m years old.

Experts believe the skull is one of the most important fossil finds to date, but it has proved as controversial as it is stunning. Analysis of the skull and other remains at Dmanisi suggests that scientists have been too ready to name separate species of human ancestors in [Africa](#). Many of those species may now have to be wiped from the textbooks.

The latest fossil is the only intact skull ever found of a human ancestor that lived in the early Pleistocene, when our predecessors first walked out of Africa. The skull adds to a haul of bones recovered from Dmanisi that belong to five individuals, most likely an elderly male, two other adult males, a young female and a juvenile of unknown sex.

The site was a busy watering hole that human ancestors shared with giant extinct cheetahs, sabre-toothed cats and other beasts. The remains of the individuals were found in collapsed dens where carnivores had apparently dragged the carcasses to eat. They are thought to have died within a few hundred years of one another.

"Nobody has ever seen such a well-preserved skull from this period," said [Christoph Zollikofer](#), a professor at Zurich University's Anthropological Institute, who worked on the remains. "This is the first complete skull of an adult early Homo. They simply did not exist before," he said. Homo is the genus of great apes that emerged around 2.4m years ago and includes modern humans.

Other researchers said the fossil was an extraordinary discovery. "The significance is difficult to overstate. It is stunning in its completeness. This is going to be one of the real classics in paleoanthropology," said [Tim White](#), an expert on human evolution at the University of California, Berkeley.

But while the skull itself is spectacular, it is the implications of the discovery that have caused scientists in the field to draw breath. Over decades excavating sites in Africa, researchers have named half a dozen different species of early human ancestor, but most, if not all, are now on shaky ground.

The remains at Dmanisi are thought to be early forms of *Homo erectus*, the first of our relatives to have body proportions like a modern human. The species arose in Africa around 1.8m years ago and may have been the first to harness fire and cook food. The Dmanisi fossils show that *H erectus* migrated as far as Asia soon after arising in Africa.

The latest skull discovered in Dmanisi belonged to an adult male and was the largest of the haul. It had a long face and big, chunky teeth. But at just under 550 cubic centimetres, it also had the smallest braincase of all the individuals found at the site. The dimensions were so strange that one scientist at the site joked that they should leave it in the ground.

The odd dimensions of the fossil prompted the team to look at normal skull variation, both in modern humans and chimps, to see how they compared. They found that while the Dmanisi skulls looked different to one another, the variations were no greater than those seen among modern people and among chimps.

The scientists went on to compare the Dmanisi remains with those of supposedly different species of human ancestor that lived in Africa at the time. They concluded that the variation among them was no greater than that seen at Dmanisi. Rather than being separate species, the human ancestors found in Africa from the same period may simply be normal variants of *H erectus*.

"Everything that lived at the time of the Dmanisi was probably just *Homo erectus*," said Prof Zollikofer. "We are not saying that palaeoanthropologists did things wrong in Africa, but they didn't have the reference we have. Part of the community will like it, but for another part it will be shocking news."

[David Lordkipanidze](#) at the Georgian National Museum, who leads the Dmanisi excavations, said: "If you found the Dmanisi skulls at isolated sites in Africa, some people would give them different species names. But one population can have all this variation. We are using five or six names, but they could all be from one lineage."

If the scientists are right, it would trim the base of the human evolutionary tree and spell the end for names such as *H rudolfensis*, *H gautengensis*, *H ergaster* and possibly *H habilis*.

The fossil is described in the [latest issue of Science](#).

"Some palaeontologists see minor differences in fossils and give them labels, and that has resulted in the family tree accumulating a lot of branches," said White. "The Dmanisi fossils give us a new yardstick, and when you apply that yardstick to the African fossils, a lot of that extra wood in the tree is dead wood. It's arm-waving."

"I think they will be proved right that some of those early African fossils can reasonably join a variable *Homo erectus* species," said [Chris Stringer](#), head of human origins at the Natural History Museum in London. "But Africa is a huge continent with a deep record of the earliest stages of human evolution, and there certainly seems to have been species-level diversity there prior to two million years ago. So I still doubt that all of the 'early Homo' fossils can reasonably be lumped into an evolving *Homo erectus* lineage. We need similarly complete African fossils from two to 2.5m years ago to test that idea properly."

The analysis by Lordkipanidze also casts doubt on claims that a creature called *Australopithecus sediba* that lived in what is now South Africa around 1.9m years ago was a [direct ancestor of modern humans](#). The species was discovered by [Lee Berger](#) at the University of Witwatersrand. He argued that it was premature to dismiss his finding and criticised the authors for failing to compare their fossils with the remains of *A sediba*.

"This is a fantastic and important discovery, but I don't think the evidence they have lives up to this broad claim they are making. They say this falsifies that *Australopithecus sediba* is the ancestor of Homo. The very simple response is, no it doesn't."

"What all this screams out for is more and better specimens. We need skeletons, more complete material, so we can look at them from head to toe," he added. "Any time a scientist says 'we've got this figured out' they are probably wrong. It's not the end of the story."

This article was amended on 18 October 2013. An earlier version incorrectly located [Georgia](#) in central Asia.

Source: <https://britannica.com/topic/Homo-erectus/Relationship-to-Homo-sapiens>

